CHANGE IN TROPHIC STRUCTURE OF A SHELF ECOSYSTEM IN THE NORTHWEST ATLANTIC DURING A PERIOD OF INCREASED FISHING PRESSURE

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CHANGE IN TROPHIC STRUCTURE OF A SHELF ECOSYSTEM IN THE NORTHWEST ATLANTIC DURING A PERIOD OF INCREASED FISHING PRESSURE

by

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Change in trophic structure of a shelf ecosystem in the northwest Atlantic during a period of increased fishing pressure.

Erin K. Alcock

Multi-species and ecosystem modelling are increasingly touted as essential approaches in the future of fisheries management. These methodologies can involve the amalgamation of data on the landings, biomass, consumption, production, and diets of many species or species groups in current time, the future and in the re-examination of the past. The Ecopath approach was used to construct two mass balance ecosystem models for the southern Labrador Shelf, Northeast Newfoundland Shelf and Grand Bank in Northwest Atlantic Fisheries Organisation (NAFO) Divisions 2J+3KLNO the first for the time period 1954-1956 and the second for 1968-1970. Our models increased the temporal resolution of ecosystem models developed by The Fisheries Centre at the University of British Columbia. The start (1950s) and rapid expansion (1960s) of industrial harvesting by factory freezer trawlers during these time periods resulted in massive increases in fishing effort, the total catch increased by 30%, and there was extensive spatial intensification and expansion, particularly on the Labrador Shelf. Biomass declines in adult and juvenile Atlantic cod, harp seals, and their main prey species capelin and sandlance were evident. A change in predator/prey relationships between the two time periods was expected, but not found. An increase in the biomass of some invertebrate species groups was expected, but not evident, possibly due to sparse historical data. System ratios and indicators pointed to the latter ecosystem as nearer to a state of being 'fished down', perhaps indicating the onset of the trophic shift evident in the late 1980s and 1990s.

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Chapter 1: Introduction

The fishery in the Northwest Atlantic Ocean off Newfoundland and Labrador, Canada has a long history, from cod allegedly slowing the progress of ships 500 years ago, to an eventual collapse of cod stocks throughout the 1970s and 1980s, culminating in a groundfish fishery closure in 1992. Reconstructing the history of changes in marine ecosystems on the east and west coasts of Canada is an ongoing process which aims to provide insights into ecological and fisheries management problems in the past and thus inform contemporary fisheries policies. One aspect of such work places ecosystem models of the Newfoundland and Labrador shelf in time periods with relevant technological and social changes. Models intended to reflect the system prior to European contact (1450/1500) and before mechanised fishing (1900) have been constructed (Heymans and Pitcher, 2002). A model for 1985-87 points to a view of the Newfoundland and Labrador shelf in the time thought to be 'pre-collapse' or at least early in the decline for groundfish populations, while a model describing the ecosystem in 1995-97 represents the 'post- collapse' period (Heymans and Pitcher, 2002). This thesis contributes to this larger project of historical reconstruction by modelling the marine ecosystems in NAFO (Northwest Atlantic Fisheries Organisation) zones 2J-3KLNO (Figure 1.1) for the periods 1954-1956 and 1968-1970. These periods bracket the onset of the international distant water fisheries in this area and the point when landings in these fisheries collapsed after 1968.

The twentieth century has been witness to vast technological change within the fishing industry. Starting with handlines and jiggers, through cod traps and gillnets, then longlining, side trawling, stern trawling and finally factory freezer trawling, humans have become exceptionally skilled at taking fish from the sea. The most common method of industrial fishing today is the stern trawler and more specifically the factory freezer stern trawler, introduced to Newfoundland waters in 1954. Even with the addition of mid-water trawls, fish finding capabilities, GPS, and improved freezing techniques, factory freezer trawlers remain unchanged in terms of their basic elements (McNamara, 1986).

In 1954, the British factory freezer trawler *Fairtry* appeared off the coast of Newfoundland to fish for Northern cod (Hutching and Myers, 1995). In each subsequent year, more foreign trawlers arrived in the area, harvesting cod, haddock, flounders and redfishes at a tremendous rate. The Northern cod landings peaked in 1968 at 810 000 metric tonnes (Hutchings and Myers, 1995, p.58) (Figure 1.2). Although many more factory freezer trawlers were active throughout the 1970s, the combined landings would never surpass the peak of 1968, even as they expanded effort spatially and ecologically. The pressure on Northern cod and many other groundfish species would eventually play a role in a large shift in the trophic composition of the ecosystem on the Newfoundland and Labrador shelf exemplified by the collapse and subsequent closure of the Northern cod fishery (Lilly, 1987).

In the years following the groundfish collapse of the early 1990s academics, governments, industry, and local fish harvesters have scrutinised fisheries and marine ecosystems to try to understand what happened. Explanations range from bad science,

and/or weak governmental decision making procedures, to environmental anomalies (Steele, *et al*, 1992, Myers and Worm, 2003 and Hilborn *et al.*, 2003). The majority of studies of this collapse have been reductionistic, often making the case for single causes. The use of multi-species and holistic ecosystem methodologies eliminates the narrow focus on single species or single causes.

Looking at natural systems from a broad perspective and finding ways to amalgamate data from detailed studies can provide a better perspective on the ecosystem than traditional single species approaches. One such approach is known as Ecopath with Ecosim 5, a mass balance modelling software originating in earlier work by Polovina (1984) and Christensen and Pauly (1992). These models estimate a balance of trophic linkages based on biomasses, productivities, consumption rates, diet compositions, and fisheries yield for each species, or species group in the chosen food web (Cox *et al.*, 2002). Based upon studies by E.P. Odum (1969) and Christensen and Pauly (1998), Ecopath also generates indices such as the Gross Efficiency which describe the stage of development in an ecosystem and the influence of fishing on the state of this development (Trites *et al.*, 2000). Ecopath can convey the importance of fishing relative to inter-species predation and has influenced the recent focus on trophic level as a functional entity, rather than a sorting tool, i.e., descriptions of the trophic levels within an ecosystem can be useful to express the distribution of feeding at all levels of the food web (Pauly *et al.*, 2000 and Pauly *et al*, 1998). The mean trophic level of an ecosystem can be used to describe changes within systems over time, particularly when components

of the system are being removed for human use and consumption; it can also be used for comparisons among ecosystems (Pauly *et al.*, 1998).

In this study I use the Ecopath mass balance modelling approach to explore immediate ecosystem effects associated with the first fifteen years of factory freezer trawler activity on the Newfoundland and Labrador Shelf. Two models are assembled, the first for the period 1954-56, representing the ecosystem at the onset of factory freezer trawler activity, and the second for 1968-70, the time of the largest catches of Northern cod, a period known as the 'killer spike' (Figure 1.2)(Hutchings and Myers, 1995). To determine if the introduction of the factory freezer trawler had an impact on the ecosystem in my study area I will compare the biomass of those species targeted by the intense international harvesting and the overall mean trophic level of the system in the late 1960s to that of the mid-1950s. I will also examine the mean trophic level of the landings to determine if the catch expanded to include species lower in the food web. Other aspects that can be compared over time include indices of resilience, resistance to perturbations and flows between ecosystem components.

Like all modelling approaches, an Ecopath mass balance model comes with assumptions and uncertainties. However, these models can serve as useful tools and are probably most helpful when users realise that no model can completely represent reality (Schnute and Richards, 2001). When interpreting any ecosystem model, it helps if the reader maintains a dose of healthy scepticism (Gomes, 1993).

In order to provide a setting for the Ecopath models a discussion of the state of the fishery before, during and after the 'killer spike' is presented in Chapter 2. The

foundation of this discussion will be international fisheries landings reported to the International Commission for Northwest Atlantic Fisheries (ICNAF) from 1953 to 1977 and to NAFO since 1978. An analysis of the international fleet provides information on targeted species, spatial changes in harvesting, diversification of landings, and other issues that may have been factors in the restructuring of the fishery of the Newfoundland and Labrador Shelf and are important to understanding and interpreting the Ecopath results. Chapter 3 outlines the approach taken to develop the Ecopath models and reviews the assumptions and rationalisations made for historical biomass estimates and derives the derivation of the other model input data. Chapter 4 outlines the results of the models and makes some comparisons between the ecosystems represented by the models in the mid-50s and late-60s. Finally, the discussion chapter, Chapter 5, reviews and interprets the model results to determine if there are any indications of the fishery collapse/shift which occurred in the 1970s, followed by some discussion of modelling limitations.

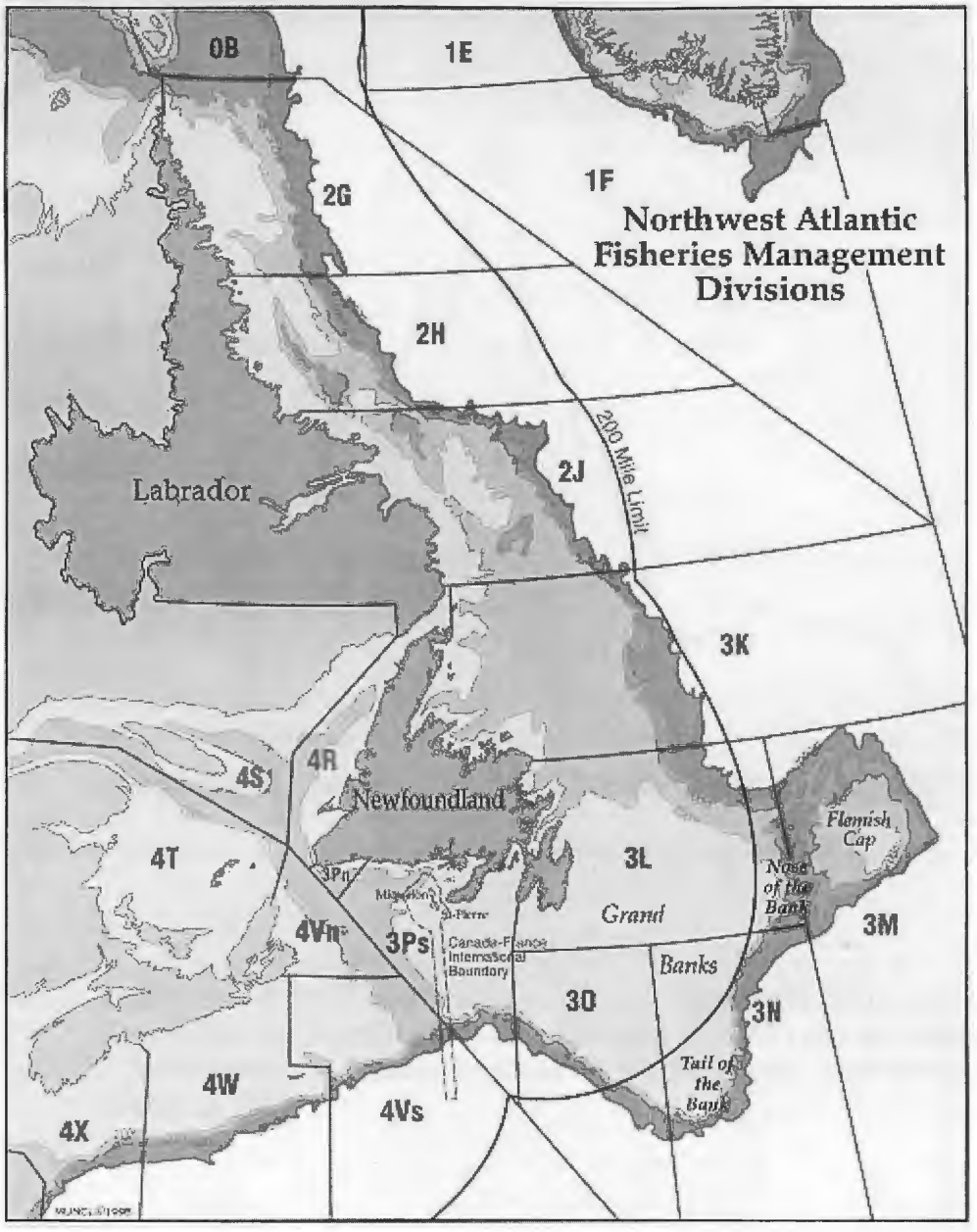


Figure 1.1: Map of the Newfoundland and Labrador shelf showing Northwest Atlantic Fisheries Organization Zones, as well as, the 200 Mile Exclusive Economic Zone (www.nafo.ca).

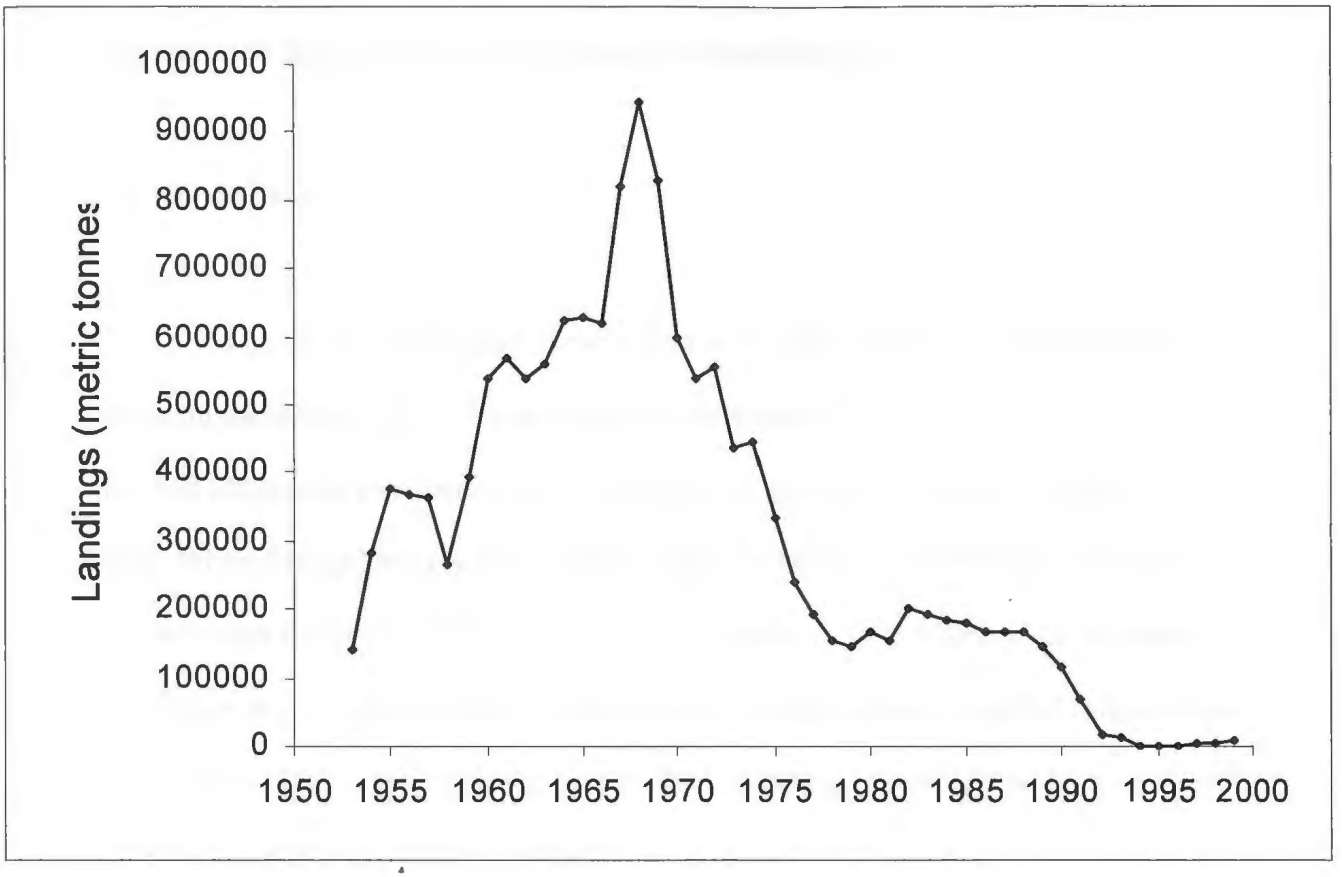


Figure 1.2 : Landings of Atlantic cod (*Gadus morhua*) as reported to the International Commission for Northwest Atlantic Fisheries (ICNAF) and the Northwest Atlantic Fisheries Organisation (NAFO), illustrating the large increase in catches in 1968.

Chapter 2: Fishery History of Newfoundland and Labrador

2.1 Introduction

There are few treatments of the history of Newfoundland and Labrador that do not focus on the fishery. The fish populations on the banks of this province were the reason the first Europeans came more than five hundred years ago to fish and eventually to live here. While fishing has been important throughout these five hundred years, this study focuses more on the first half of the twentieth century, to set the context on the state of the fishery prior to the arrival of the factory freezer trawler fleets. Detailed information on the state of the fishery between the two time periods portrayed by the Ecopath models and shortly after will also be provided.

2.2 The fishery prior to 1954

After European discovery of North America in the late 15th century, the English, French and Portuguese vied for control in different regions of the island of Newfoundland. By the end of the 19th century the English dominated most of the coastal settlements (Parsons, 1993). Fishers from these countries came to stay for the fishing season and eventually settled to form communities. Settlers and migratory fishers fished the shores near their settlements and on the Grand Banks. As fishing gear improved, they

began moving away from their communities into newer waters, farther offshore and farther north, to Labrador (Hutchings and Myers, 1995). The main species of interest was Atlantic cod, though haddock, flatfish species, capelin, herring and lobster were all caught where available (ICNAF, 1950). All fishery sectors, including government, particularly following the Second World War, were interested in modernisation and expansion, under the assumption that resources from the sea had no limit (Parsons, 1993).

Looking back, many acknowledged that local inshore populations of cod appeared to have been over-fished as early as the late 1800s (Cadigan, 1999). However much of the literature relating to fisheries history considers the fishery in Newfoundland and Labrador to have been sustainable prior to the 1950s (Hutchings and Myers, 1995). With the large increase in effort offshore by foreign nations and domestic fishing vessels in the 1950s, some scientists, policy makers and many local fishers began advocating conservation (Wright, 1995). Scientists started to acknowledge that the inshore cod harvested by local fishers and the offshore cod taken by larger ships were not two completely different pools of fish. Wilfred Templeman, the long time director of the Fisheries Research Board of Canada in Newfoundland, observed that offshore intensification of effort was likely one of the main reasons for much of the decline in inshore landings. However, he also acknowledged that fisheries science really did not have sufficient evidence to completely understand the dynamics of the offshore component of the cod on the Newfoundland and Labrador shelf (Wright, 1995).

Fisheries on several species other than Northern cod experienced peaks and subsequent declines quite early in the new industrial fishing phase. Haddock, fished very

sparsely off Newfoundland and Labrador before the early 1940s, experienced its first significant decline in landings in 1949 (Templeman, 1966). More than other nations, Spain increased effort throughout the 1950s, following World War Two. The second collapse in the landings of haddock occurred in 1962 (ICNAF and NAFO 1963). Redfish species are long lived, live bearing fish and require special conservation efforts (Fishbase, 2004). A peak in redfish landings reported by ICNAF (International Commission for the North Atlantic Fisheries) occurred in 1959 at over 240 000 metric tons. After 1962 redfish landings remained well below this peak, rarely going above 80 000 metric tons, in spite of intense harvesting effort by the USSR. Templeman's statements of uncertainty about the Northern cod stocks would imply that much more uncertainty would have existed about the states of many other species and populations in the area, populations which would become important components of international catches over the next decades.

2.3 The fishery between 1954 and 1970

The first factory freezer trawler (FFT), the British registered ship *Fairtry*, arrived in Newfoundland waters in 1954. All future generations of factory freezer trawlers during this period were based upon the same basic design as the *Fairtry* (Warner, 1983). Mowat (1984) describes the surprised reactions of crew members on the *Fairtry*, who in 1956 saw an identical ship, the *Pushkin* from the USSR, on the horizon, after just two years of being on their own on the Grand Banks. The *Fairtry* could harvest up to 4.4

million pounds of fish in only 37 days and with the processing equipment on board, most factory freezer trawlers had about a 70 day range away from their home ports (McNamara, 1986). They were also considered safer than many other methods of offshore fishing, in particular, trawling over the side of a boat (side trawling) or dory fishing from a schooner as in the Grand Banks fishery (Warner, 1983).

The geographic distribution of the FFT fishery did not remain constant throughout the 1950s and 1960s. Figure 2.1 illustrates the amount of the commercial landings that were harvested in each NAFO zone during this period. Early FFT activity took place mostly on the Grand Banks (3LNO) and off the northeast coast of the Island (3K), with only 5% of the landings coming from off the coast of Labrador (2J). By the late 1950s, 2J was the most important zone in terms of the percent of total landings. The significance of the fishery off Labrador parallels the importance of the Labrador fishery throughout the nineteenth century. Up to 46% of the total landings from the area came from Labrador in 1890 (Hutchings and Myers, 1995). In the past, these were inshore and near-shore landings made by residents of Conception and Trinity Bays who travelled to Labrador during the summers (Hutchings and Myers 1995). After 1970 (not included in Figure 2.1), the significance of the FFT fishery off Labrador decreased (NAFO, 2003).

Many new countries participated in the 2J 3KLNO fishery throughout the 1960s and those that had been fishing off Newfoundland and Labrador previously intensified their effort, including the Newfoundland fleet. Figure 2.2 illustrates the total landings in NAFO Zones 2J3KLNO between 1953 and 1978 divided into the amounts taken by each fishing nation. The landings by the USSR increased through time, whereas landings by

Canada and Spain were consistent and high. By 1960, the USSR was a very significant force in the fishery on the Newfoundland and Labrador shelf. Although Soviet representatives visiting St. John's in the early 1950s, stated that they were mainly interested in fishing redfish and that they could get cod and haddock elsewhere (Warner, 1983). USSR FFTs caught significant amounts of Atlantic cod, haddock and American plaice during this time period and continued to diversify their catch through the 1970s (NAFO, 2003). The number of Soviet vessels increased from two in 1956 to thirty five in 1958 (Warner, 1984) and in 1965 the USSR fleet off Newfoundland was comprised of 106 factory freezer trawlers, 30 mother ships and 425 side trawlers (McNamara, 1986). The year 1959 was a significant year in the history of the FFT fishery as it was the first year that offshore catches of Northern cod exceeded inshore catches. 1959 was also the first year since the 1700s when catches by resident Newfoundlanders did not exceed those of all other participants in the fishery (Hutchings and Myers, 1995) due in part to the expansion in the Soviet fleet.

There are some major differences in the fisheries on the Newfoundland and Labrador shelf over this time period. In 1954-56 five countries reported landings (note that Newfoundland has been considered separately from the rest of Canada). Newfoundland and Portugal were responsible for most of the landings in this time period. By 1968-70 several new countries had become involved in the fishery of the area, including the USSR, the German Democratic Republic, Iceland and Spain, and harvests were high.

Atlantic cod, the most important species in the fishery of the Newfoundland and Labrador shelf, continued to be important throughout the 1950s, 1960s and 1970s. Figure 2.3 illustrates landings by species. In 1954-56, haddock and redfish were the only other two species that were clearly being targeted by fishing nations, or were recorded by ICNAF. By 1968-70, landings of American plaice, yellowtail flounder, witch flounder and Greenland halibut had all increased, with cod and redfish still notable. It is likely that many of these species had also been caught as bycatch in the earlier years of factory freezer trawler activity and/or had not been reported, i.e., most flounder species were reported to ICNAF in one category before 1960 after which American plaice, witch flounder and yellowtail flounder were recorded as individual species (ICNAF, 1960).

In the years following the arrival of the FFTs, there were increased calls for a more thorough look at the dynamics of the fish populations before the domestic fishery expanded further (Wright, 1995). It was difficult to convince many of the decision-makers that the increased fishing activity offshore was seriously affecting the landings by inshore harvesters. Joey Smallwood, then premier of Newfoundland and Labrador, stated at a provincial fisheries conference in 1962, that he was more interested in doubling the productive capacity of the provincial offshore fleet (Wright, 1995). Colin Story, a long time employee of the Department of Fisheries contended in 1958 that part of the problem was the large scale at which early international statistics were gathered. Bonavista, for example, fell within ICNAF statistical zone 3L. The size of 3L made it difficult for individuals in a place like Bonavista to 'see' the relationship between inshore and offshore cod (Wright, 1995). Canada attempted to establish exclusive rights to the waters

adjacent to Newfoundland and Labrador but it was only after three tries at Law of the Sea Conferences (1958, 1960 and 1964), that Canada established a 12-mile fishing limit. However, foreign nations with "historic" rights were still permitted to fish within this zone (Wright, 1995).

2.4 The Newfoundland and Labrador Fishery in the 1970s and Some Issues with Fisheries Data

Much happened after the 'killer spike' in Northern cod landings in 1968 (Hutchings and Myers, 1995). With the introduction of the midwater trawl by the German Democratic Republic in 1969, landings became more diverse, with a notable increase in landings of pelagic species. The biggest change was the increase in capelin landings, attributable mostly to the USSR and German Democratic Republic (Figures 2.2 and 2.3).

Boreman *et al.* (1997) list the peak landings for many groundfish and flounder landings throughout the 1960s and 1970s. They contend that most true groundfish species had peaked before 1968, while flatfish species like witch and yellowtail flounder did not experience their peaks until early in the 1970s. The move to pelagics would come after this. This is evident in the landings data provided by NAFO (2003) (Figure 2.3).

Generally, landings data do not provide an accurate picture of the true abundance of the species in consideration. They are imprecise indicators of abundance as they provide no reflection of changes in efficiency or spatial expansion, especially when

considered over short time periods (Sinclair and Murawski, 1997). However, commercial groundfish landings over longer time periods often correlate well with indices of abundance (Sinclair and Murawski, 1997). Hutchings and Myers (1995) note a high degree of variability within research survey data and, while catch data has its problems, such data are often all we have to work with and can be valuable at larger spatial and temporal scales. The government of Canada used catch rates as indices of abundance until 1988 (Hutchings and Myers, 1995).

Historical catch data may have greater flaws due to misreporting and the probability of substantial and varying discarding activity, a problem that persists in fisheries today (Hall *et al.*, 2000). Fish with low market value have traditionally been dumped and gone unreported throughout the history of fisheries. Ironically, some of the species discarded during the 1950s became commercially or ecologically valuable over the next decades. Snow crab, a very important commercial species in Newfoundland and Labrador since the early 1990s were commonly stomped on before being tossed overboard to help remove them from gill nets set to catch cod. By the late 1960s, it has been suggested that over 50% of the estimated harvestable biomass of Northern cod was landed in each year, though this is likely an underestimate due to discarding of bycatch (Hutchings and Myers, 1995). Plants processing cod in Newfoundland and Labrador refitted much of their equipment throughout the 1980s to accommodate smaller fish, i.e., 'smaller' cod had become a larger component of commercial landings (Ings, D. *pers.comm,* 2004).

In 1971, ICNAF's stated goal was to maximize utilization of fish stocks, i.e., they utilized the principle of Maximun Sustainable Yield (MSY). MSY is the largest catch that can be removed under existing environmental conditions over an indefinite period without causing the stock to become depleted (Hilborn and Walters, 1992). Throughout the 1950s and 1960s there was interest in conservation but no significant action occurred until 1977 when Canada extended its authority to the 200 mile Exclusive Economic Zone (Steele *et al*, 1992). This drastically reduced the heavy fishing by foreign nations on the Newfoundland and Labrador shelf and Canada set about their stated goal of rebuilding the Northern cod stock (Steele *et al*., 1992). Unfortunately, 1977 may have been too late to protect or rebuild, though there might have been a better chance had abundance of the Northern cod stock not been repeatedly overestimated during the late 1970s and early 1980s (Kirby, 1984 and Finlayson, 1994), which lead to a rapid increase in domestic fishing effort through the 1980s. As a result the positive effects of the Exclusive Economic Zone were mitigated by rapid expansion in domestic fishing effort (Steele *et al*., 1992).

The history of these fisheries provides the context for the mid-1950s and late-1960s Ecopath models. Understanding the development of the fisheries, particularly with respect to offshore development, will help in the interpretation of model results for the ecosystem off east and northeast Newfoundland and Labrador between 1954 and 1970.

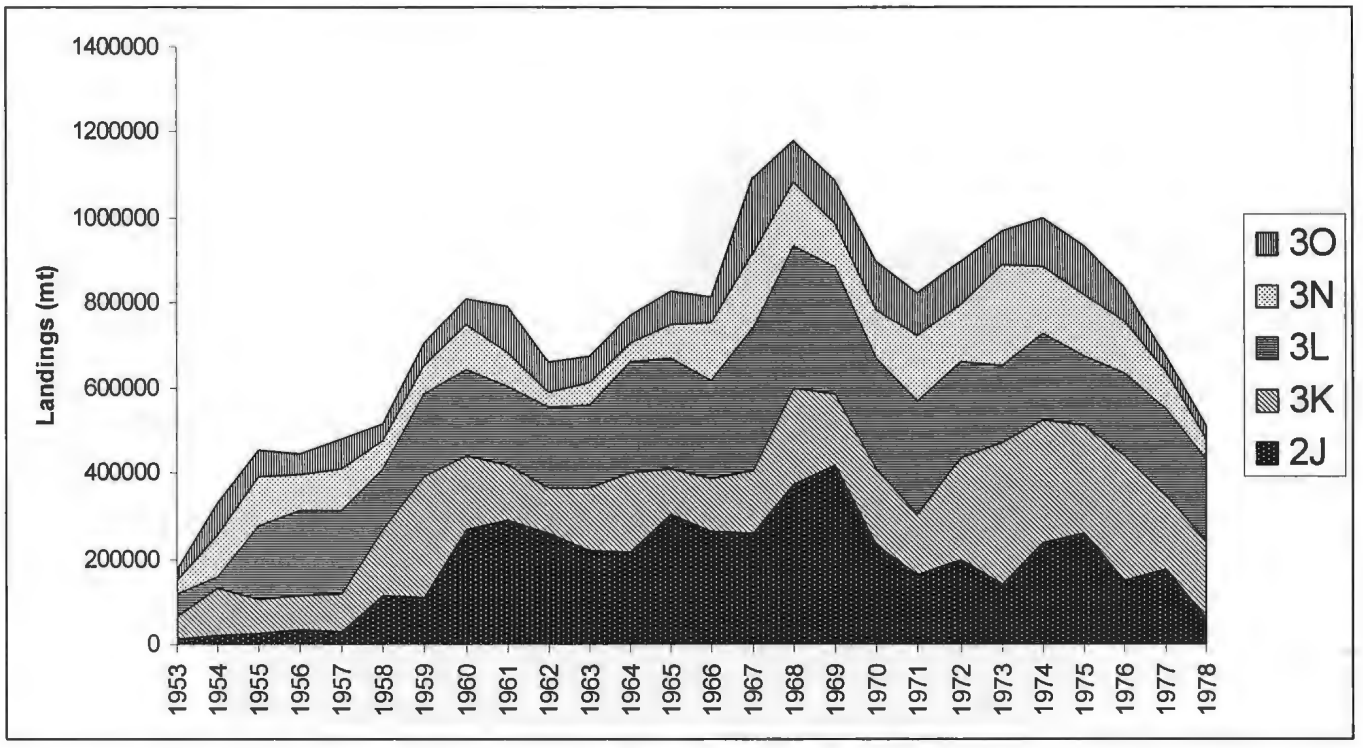


Figure 2.1: Landings reported to the International Commission for the Northwest Atlantic Fisheries and the Northwest Atlantic Fisheries Organisation divided into the landings taken in each NAFO zone, illustrating the shift to 2J (www.nafo.ca).

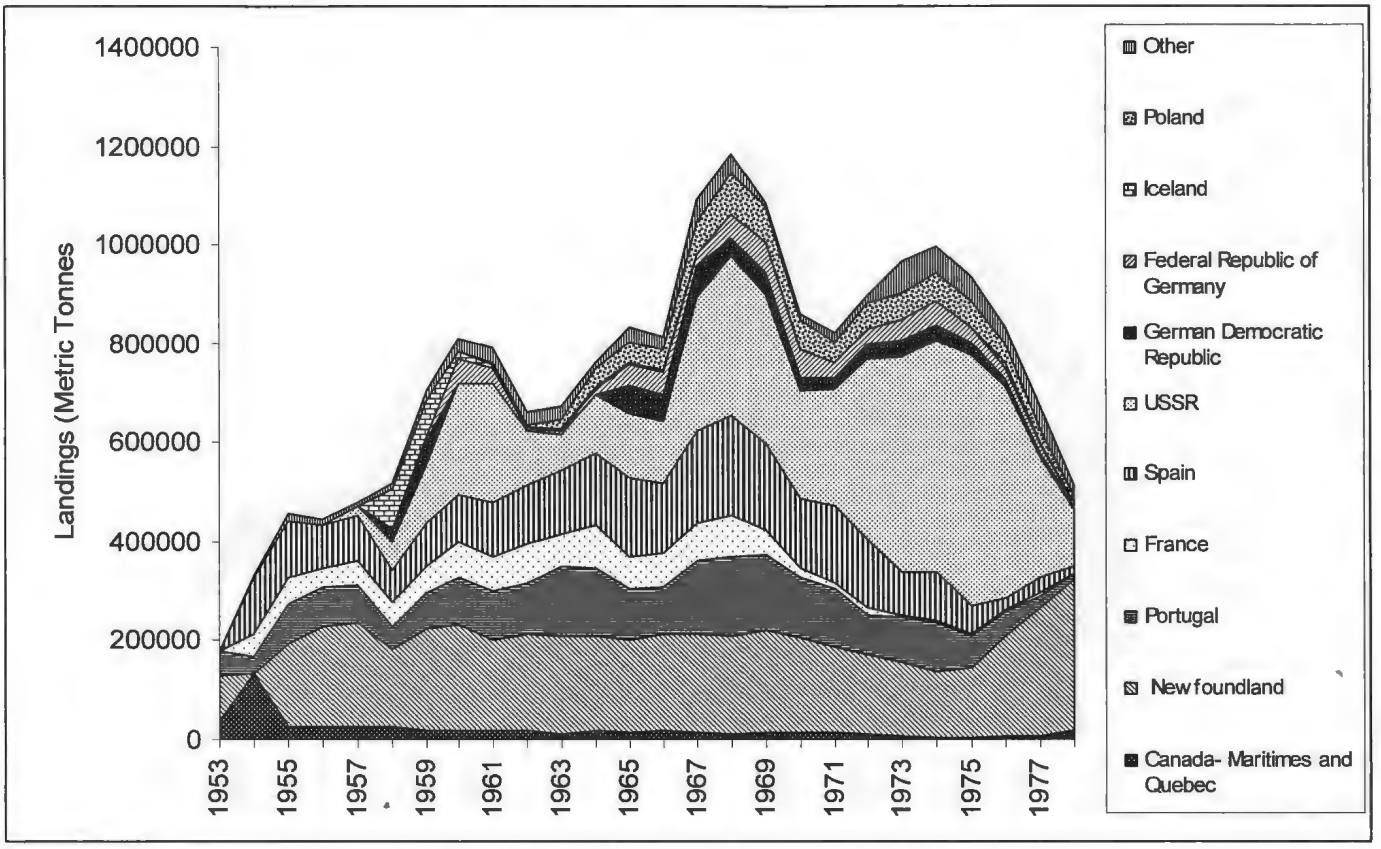


Figure 2.2: Commercial Fisheries Landings (in metric tonnes) reported to the International Commission for Northwest Atlantic Fisheries between 1953 and 1978, taken by the major fishing nations (Other: Countries include Cuba, Norway, Ireland, USA, Unted Kingdom, Japan, Romania, Denmark, the Faroe Islands, St. Pierre and Miquelon, Bulgaria, and Israel).

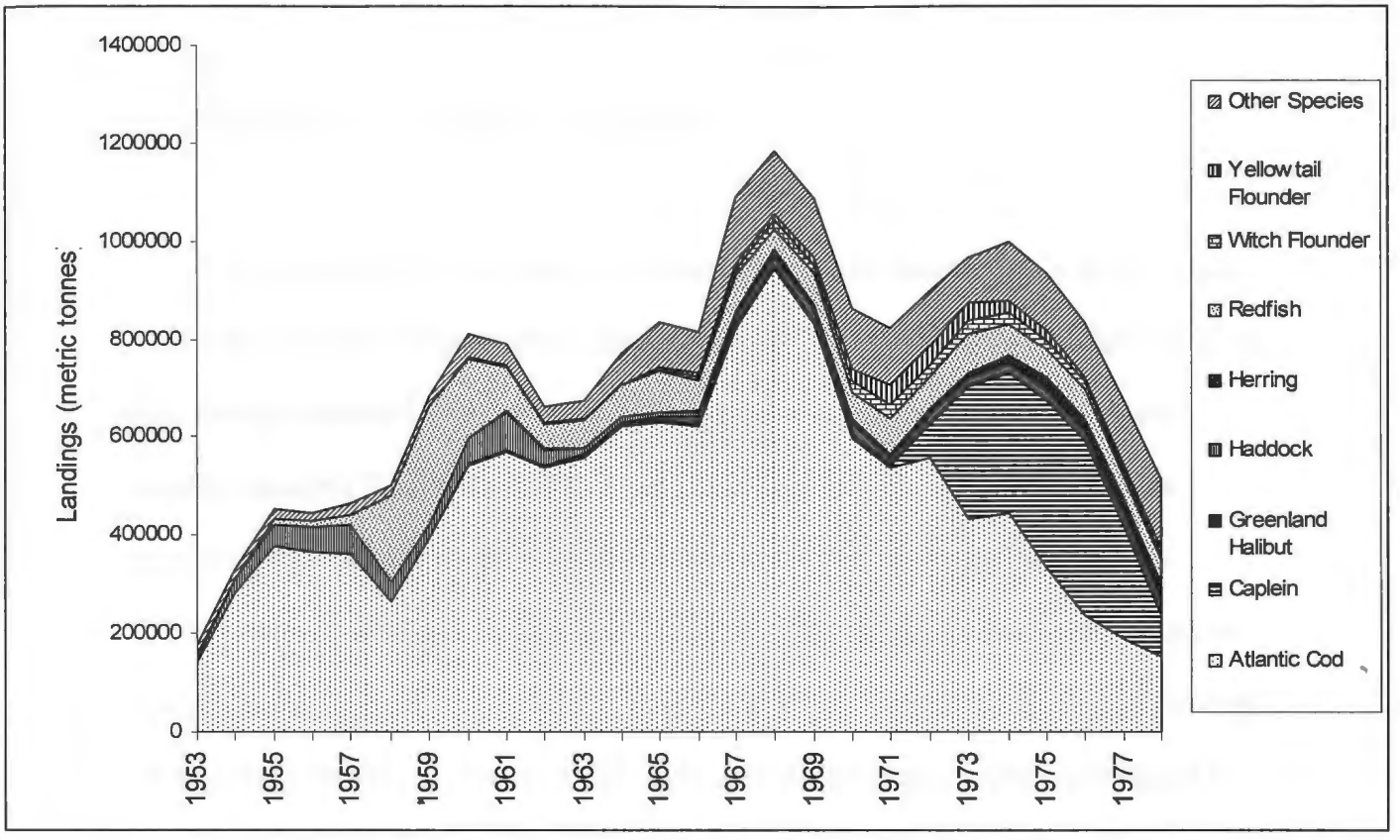


Figure 2.3: Commercial Fisheries Landings reported to the International Commission for Northwest Atlantic Fisheries between 1953 and 1978, divided by species (Other Species include: American eel, American plaice, angler, argentines, Atlantic halibut, Atlantic salmon, Atlantic saury, blue mussel, bluefin tuna, cusk, dogfish, eelpouts, large sharks, ling, lobster, lumpfish, lackerel, northern prawn, pollock, porbeagle, red hake, roundnose grenadier, sandeels, sea scallop, sculpins, shortfin squid, silver hake, skates, smelt, spiny dogfish, swordfish, white hake, winter flounder, wolffish and non-specified chars, finfish, flatfish, flounders, groundfish, pelagics, shellfish, shrimps, trouts and tunas).

Chapter 3: The model and how it works/ Methods

3.1 Mass Balance and the Ecopath Approach

The principle of mass balance is commonly used in science and is familiar from chemical equations where products equal reactants. Energy consumed by heterotrophs (or light energy converted by autotrophs), is transformed into fixed carbon, thus mass balance can apply (Campbell, 1993). Mass balance can also be used to describe an ecosystem at a steady state for a given time period and has been applied widely to terrestrial and aquatic systems (Trites *et al.*, 1999). Discussions of mass balance and its relationship to food web dynamics in aquatic ecosystems have been ongoing for most of the twentieth century; Lindeman (1942) undertook the first mass balance analysis of an ecosystem and summarised some early ecological theories from terrestrial and aquatic ecosystems, from a tropho-dynamic perspective.

In general, a mass balance model of a fisheries system can be represented by the following equation:

$$\textit{Production} = \textit{Biomass Accumulation} + \textit{Fisheries Catch} + \textit{Mortality Due to Predation} + \textit{Other Mortality} + \textit{Loss to Adjacent Systems},$$

for any producer in the time period being considered. Each species or species group is linked in a predator/prey relationship in which:

Consumption = Production + Non-assimilated Food + Respiration

The model is established when the system of equations is solved for each species group (Christensen *et al.,* 1992).

More specifically, the necessary condition in the Ecopath approach for mass balance is defined by the following equation:

$$P_x - M0_x - M2_x - C_x = 0 \quad (1)$$

Where

P_x = the annual biomass produced by species x ($t \cdot km^{-2} \cdot year^{-1}$)

$M0_x$ = annual biomass loss of species x not accounted for by any other predator group included in the model nor by catch or export, that is other mortality ($t \cdot km^{-2} \cdot year^{-1}$)

$M2_x$ = annual biomass of species x consumed by all predator groups included in the model, i.e., "predation mortality" ($t \cdot km^{-2} \cdot year^{-1}$)

C_x = annual catch of species x ($t \cdot km^{-2} \cdot year^{-1}$)

$M2x$ is the sum of the annual consumption of species group x by all y predators that are included in the model:

$$M2_x = \Sigma p_{xy} Q_y \quad (2)$$

where

p_{xy} = proportion by mass of predator y's diet that is comprised of prey x

Q_y = the annual consumption of biomass ($t \cdot km^{-2} \cdot yr^{-1}$) by predator y

M0, or other "unexplained" mortality, in Ecopath is expressed as 1- EE_x where EE_x is the ecotrophic efficiency, or the proportion of P_x that is not consumed by predators included in the model or caught by a fishery:

$$EE_x = (M2_x + C_x)/ P_x \quad (3)$$

These relationships permit a set of simultaneous linear equations that can be solved to balance the ecosystem model. The production and consumption (both expressed in $t \cdot km^{-2} \cdot yr^{-1}$) terms are scaled by biomass (in $t \cdot km^{-2}$), that is, they are expressed as ratios (*P/B* and *Q/B*). *M0* and *M2* are annual rates of mortality. Equation (1) is solved for each species or species group in the model. Each equation requires six input parameters; diet composition and catch, if applicable, and three out of four of biomass (*B*), production/biomass (*P/B*), consumption/ biomass (*Q/B*) and ecotrophic efficiency (*EE*). As the equations are solved, the parameters that are lacking can be estimated by Ecopath. Ideally, only the ecotrophic efficiency term is estimated, that is, the model is more robust when values for *B*, *P/B* and *Q/B* are entered. However, in data scarce situations, a default value of 0.95 is entered for *EE* (*EE* is between 0 and 1), thus allowing for an estimate of one of the other parameters, often biomass. *EE* is expected to be close to 1 for species

under heavy fishing pressure, heavy predation pressure or both (Christensen and Pauly, 1992; Bundy *et al.*, 2000).

3.2 Parameter Estimation

Parameters were estimated or obtained for fifty species groups; species groups were defined in terms of their commercial significance, their importance as predators or prey or both (Bundy *et al.*, 2000) See Table 3.1 for Species Groups in this study. These models include all major groups ranging from detritus to cetaceans, including plankton, shellfish, fish, seabirds, and seals. The fifty species groups are consistent with models of the Newfoundland and Labrador shelf developed by Heymans and Pitcher (2002) to permit overall comparability. Adult and juveniles within important species groups are separated to indicate dietary and physiological differences (Heymans and Pitcher, 2002). The significance of many species may have changed during the period covered. Snow crab, for example, might warrant its own species group (apart from other crab species in more recent models) as its significance to the fishery increased in more recent times.

3.2.1 Biomass

Biomass estimates B ($t \cdot km^{-2}$) were calculated by Ecopath for 37 of 50 species groups in the model for 1954-56 (mid-1950s model) and for 36 of 50 in 1968-70 (late-1960s model). The ecotrophic efficiency (EE) was assumed to be 0.95 for those groups so

that the software would estimate a value for biomass. The time frame of these two models predates trawl surveys, hydro-acoustics, and valid data for sequential population analyses. In the absence of other historical records, indications of biomass (*B*) for many species are difficult to ascertain. When estimates of biomass (*B*) were available, they were entered directly, leaving ecotrophic effiency (*EE*) to be estimated.

Walrus (*Odobenus rosmarus*), included in the mid-1950s and late-1960s models, both covering a geographic area of 495000km^2 (Heymans and Pitcher, 2002), was mainly extirpated from the Western North Atlantic by 1900 (Ganong, 1904) and were therefore incorporated with the lowest possible biomass of 0.00001t·km^{-2} in both time periods.

With cetaceans, I took an educated guess. Pitcher *et al.* (2002) suggested that the biomass of whales in the early 1900s was probably twice that in the late 1990s. The biomass of cetaceans included in the 1980s model by Heymans and Pitcher (2002) was obtained from Bundy *et al.* (2000). The biomass estimate for cetaceans was taken to be between these two numbers, i.e., the biomass of whales in the 1950s is estimated at 0.35t·km^{-2}, and slightly less in 1968 at 0.3t·km^{-2}, continuing the overall decline. Commercial whaling throughout the 1950s and 1960s was almost negligible, as the stocks of several species had been reduced during the early part of the century. There was a mild resurgence in whaling and processing in the late 1960s, with involvement of Japanese corporations, though this was halted in 1972 when the Canadian government placed a moratorium on whaling (Sanger, 1998).

Historically, there were moderately sized grey seal (*Halichoerus grypus*) populations in the area of NAFO Zone 2J, southern Labrador. According to Mowat

(1984) these populations had declined substantially by the start of the nineteenth century. Heymans and Pitcher (2002) used a value of 0.000001t·km^{-2} in their 1900 model and this value was also used here in the mid-1950s and late-1960s models.

The size of the harp seal (*Phoca groenlandica*) population of 2J3KLNO in the 1980s was quite well studied and is estimated to have been around 0.184t·km^{-2} (Bundy *et al.*, 2000). Pitcher *et al.* (2002) suggest the total harp seal population in the North Atlantic around 1900 was between 6 and 12 million individuals. Assuming an average weight of 130 kg each (Anonymous, 2000), and that the Newfoundland-Labrador Shelf portion was ¼ of the total population, gives a biomass of 0.591t·km^{-2} for the early 1900s (Pitcher *et al.*, 2002). A conservative estimate of 0.300t·km^{-2} was used in the mid-1950s model, and a lower estimate of 0.250t·km^{-2} in the late-1960s model; these estimates fit the trend existing between the 1900 and 1980s model.

An estimate for hooded seals (*Cystophora cristata*) was made following the harp seal example. Pitcher *et al.* (2002) suggested the biomass of hooded seals in the early 1900s was approximately three times that of the mid-1980s, or 0.102t·km^{-2}. The biomass for hooded seals entered in the mid-1950s model was 0.065t·km^{-2} and for the late-1960s model, 0.04t·km^{-2}.

Seabird populations in the northwest Atlantic have fluctuated considerably during the past century responding to human disturbance and exploitation, as well as, natural oceanographic and climatic fluctuations (Diamond *et al.*, 1993; Nettleship & Birkhead, 1985; Brown, 1991). Data deficiencies, similar to those in fisheries data, are a problem in estimating historical seabird biomasses (Diamond *et al.*, 1993). Biomass estimates for

1450 and 1900 made by Heymans and Pitcher (2002) were based on an assumption that 3% of the colonies from the North Atlantic are occupied at present (Mowat, 1984 and Montevecchi and Tuck, 1987). Colony estimates are of little utility in the northwest Atlantic because of the preponderance of migratory non-breeders, notably shearwaters and dovekies (Diamond *et al.,* 1993). In an Ecopath model of the Newfoundland and Labrador shelf for the mid-1980s, Bundy *et al.* (2000) amalgamated data from more than ten different publications on seabird species from the area, organising them according to occupation dates, population numbers and body masses. Heymans and Pitcher (2002), in modifying the Bundy *et al.* (2000) model, categorised seabirds into three separate groups; ducks, piscivorous birds, and planktivorous birds and these groups also were applied to the mid-1950s and late-1960s models (Appendix 2). The biomass values entered for the mid-1950s and late-1960s models were $0.0002t \cdot km^{-2}$ for ducks, $0.010t \cdot km^{-2}$ for piscivorous birds and $0.002t \cdot km^{-2}$ for planktivorous birds, estimates in the range of those indicated between 1900 and 1980s models (Heymans and Pitcher, 2002).

One of the main resources used by Bundy *et al.* (2000) in determining the biomass of seabirds in the mid 1980s was a report on the energy demands of seabirds by Diamond *et al.* (1993). In this study, Diamond *et al.* (1993) suggest that areas of comparable size and oceanography in the northern hemisphere support seabird populations that harvest similar amounts of energy from the marine environment. Diamond *et al.* (1993) report energy demands for seabirds from the entire western north Atlantic; the values from the southern Labrador Banks and Newfoundland Banks (the approximate equivalent of NAFO 2J-3KLNO) sum to $18.41KJ \cdot m^{-2} \cdot$year and are about

twice the value of 9.56 $KJ \cdot m^{-2} \cdot$year reported as energy required by seabirds in the Bering Sea by Schneider and Shuntov (1993). The biomass of seabirds in the Bering Sea reported by Schneider and Shuntov, 0.019 $t \cdot km^{-2}$, is similar to that used in this model (0.0122 $t \cdot km^{-2}$). Because marine birds are endotherms, estimates of energy required are closely tied to biomass. Given this and the energy requirements estimated by Diamond *et al.* (1993), it appears that the estimate of Bundy *et al.* (2000) was on the low side.

Hutchings and Myers (1995) provide an estimate of harvestable Northern cod (*Gadus morhua*) biomass prior to the offshore dominated catches of the 1960s. Heymans and Pitcher (2002) use this value as the biomass of cod in both their 1900 and 1450 Ecopath models. This value of 8.162$t \cdot km^{-2}$ is a reasonable starting point for the time period represented in the mid-1950s model, though I must acknowledge that this might produce a distorted picture of the biomass of cod prior to industrial harvesting. The use of the same value for the biomass of Atlantic cod by Heymans and Pitcher (2002) for their historical models assumes that the biomass of Atlantic cod had remained constant through 500 years of harvesting. In the late-1960s model the value entered was based on the assumption that the first fifteen years of factory freezer trawler activity harvested a tremendous amount of cod, and that the biomass may have been reduced by half, i.e., 4.00$t \cdot km^{-2}$. Estimates of juvenile cod biomass in other historical Ecopath models were estimated by assuming the same rate of change of adult biomass applied to juveniles, or the historic biomass was four times that of the 1980s (Bundy *et al.*, 2000). Therefore, the biomass of juvenile cod in 1900 was estimated as 1.360$t \cdot km^{-2}$, slightly less than one quarter of the Hutchings and Myers (1995) estimate; this was also the value used in the

mid-1950s model. The late-1960s model approximation was the same proportion of the adult estimate, or $0.6t \cdot km^{-2}$. Adult and juvenile cod are ecological cornerstones on the Newfoundland and Labrador shelf, i.e., they are very important as predators and prey.

Heymans and Pitcher (2002), include a biomass of adult and juvenile Greenland halibut (*Reinhardtius hippoglossoides*) in the model for 1900. This is based upon doubling the initial stock biomasses estimated from VPA (Virtual Population Analysis) by Bowering (2001). However, they allowed Ecopath to calculate the biomass of adults in the 1980s (See Appendix 2 and Figure 4.1). Biomass estimates for the mid-1950s model were set conservatively as $0.55t \cdot km^{-2}$ for adults and $0.40t \cdot km^{-2}$ for juveniles. Juvenile (<65cm) Greenland halibut was one of the few species groups whose biomass increased from 1900 to the 1980s (Pitcher *et al.*, 2002), and so both adult and juvenile Greenland halibut biomasses were estimated as $0.45t \cdot km^{-2}$ in the late-1960s model.

Skates are another species group with adequate information to allow for a rough estimate of biomass. Vasconcellos *et al.* (2002) suggested that the biomass of skates in the early 1900s was likely higher than in the 1980s, due to the amount that were discarded once trawlers began reporting such information. They propose that the biomass of skates in 1900 was twice the number calculated in the 1980s, $0.469t \cdot km^{-2}$ (Heymans and Pitcher, 2002). The estimated biomasses for skates in the mid-1950s and late-1960s models were $0.32t \cdot km^{-2}$ and $0.27t \cdot km^{-2}$, respectively.

Heymans and Pitcher (2002) used a biomass of $16t \cdot km^{-2}$ for capelin (*Mallotus villosus*) in both of their historical models (1450 and 1900). This is based on Carscadden *et al.* (2001), which suggests that before 1970 capelin contributed 4.6 million tonnes to

the diets of cod, seals and whales (Heymans and Pitcher, 2002). Biomass is calculated using this value as a lower limit for capelin production and an estimate of natural mortality, $0.6yr^{-1}$ (Heymans and Pitcher, 2002). Heymans and Pitcher (2002) recognize that this value does not include capelin consumed by other fish species, nor by seabirds and may be a poor estimate. The mid-1950s model has a smaller estimate of capelin biomass, $14t \cdot km^{-2}$, and in the late-1960s model, $13.5t \cdot km^{-2}$ both of which are points on the downward trend in biomass for this species from 1900 to the mid- 1980s.

The final biomass term to be entered is for detritus. Detrital biomass is calculated based upon an equation by Pauly *et al.* (1993) which relates this biomass to the primary productivity in the system and the euphotic depth:

$$\log_{10}D = -2.41 + 0.954\log_{10}PP + 0.863\log_{10}E \quad (4)$$

where

D = detritus standing stock ($gC \cdot m^{-2}$)

PP = primary productivity ($gC \cdot m^{-2} \cdot year^{-1}$)

E = euphotic depth (m)

Much of the work done on light attenuation on the Grand Bank comes from the 1980s. The mean annual euphotic depth was calculated at 54.7m by Bundy *et al.* (2000), using numbers from these studies (Hollibaugh and Booth, 1981). Bundy *et al.* (2000) gathered estimates on primary productivity on the Grand Bank and from the Labrador Shelf

ranging from 155.6gC·m^{-2} to 426gC·m^{-2} from a study by Prasad and Haedrich (1993). Plugging these values into Equation (4) results in a range in biomass from 14.9gC·m^{-2} to 38.9gC·m^{-2}, which were multiplied by a conversion factor of 10g wet weight = 1gC (Christensen and Pauly, 1992), to get 149t·km^{-2} to 389t·km^{-2}, respectively. Bundy *et al.* (2000) used the maximum of this range as the biomass for detritus in their model of the Newfoundland and Labrador Shelf in the mid 1980s.

Heymans and Pitcher (2002) calculated detritus biomass using the same method, but had trouble in balancing the model which was attributable to assuming a 95% ecotrophic efficiency in estimating phytoplankton biomass, thus influencing the primary productivity term in the detritus calculation. Attempting to balance the model they reduced the *EE* term to 0.5 which recalculated phytoplankton biomass and changed the value for primary production in Equation (4). It is clear that a default value for detritus biomass, one at least large enough to satisfy the diet requirements of the detritivores in the system, must be entered. Then, the model was run and balanced in order to obtain a phytoplankton biomass that can be converted into primary production and subsequently used in a more consistent calculation of the detritus biomass. A default value of 350t·km^{-2} was used in the running of the mid-1950s and late-1960s models. Once the models were run and balanced, the phytoplankton biomass calculated by assuming 50% ecotrophic efficiency was multiplied by the P/B ratio and this value was plugged into Equation (4) to calculate a detritus biomass of 512.9t·km^{-2} for the mid-1950s model and 467.73t·km^{-2} for the late-1960s model.

3.2.2 Production

If a steady state is assumed production should be equal to fishing plus natural mortality. Therefore, Production/Biomass (*P/B*) is assumed equal to *z*, or total mortality, (Bundy *et al.*, 2000; Allen, 1971). In the mid-1950s and late-1960s models, *P/B* values were assumed to be the same as those in a previous model for 1900 built by Heymans and Pitcher (2002). The values are an amalgamation of calculations based on many different studies, but generally they were calculated using the following equation from Palomares and Pauly (1998):

$$\log_{10}M = 0.0066 - (0.279 \cdot \log_{10}(L_\infty)) + (0.65431 \cdot \log_{10}(K)) + (0.4631 \cdot \log_{10}(T)) \qquad (5)$$

where

M = natural mortality ($year^{-1}$)

L_∞ = mean asymptotic length (cm), or the mean length the fish would reach if it were to grow indefinitely

K = the rate ($year^{-1}$) that L_∞ is approached

T = temperature in °C

Growth parameters, K, L_∞ and temperature T, were obtained from Fishbase (Froese and Pauly, 2000) (Pitcher *et al.*, 2002). Parameters for non-fish species were based upon the

mid-1980s model by Bundy *et al.* (2000). *P/B* values for all species groups were transferred from the model for 1900, though some were changed during the balancing stage to correspond with mortality in the systems of the mid-1950s and late-1960s.

3.2.3 Consumption

Consumption/Biomass *Q/B*, assumed to be the same as in 1900, was also calculated (Heymans and Pitcher, 2002):

$$\log_{10}Q/B = 7.964 - 0.204 \log_{10}W_{\infty} - 1.965T' + 0.083A + 0.532h + 0.398d \quad (6)$$

where

W_{∞} = Mean asymptotic weight (g), calculated from the length-weight formula $W(g) = a^* L^b$, values obtained from Fishbase (Froese and Pauly, 2000);

A = Aspect ratio, calculated from $A= h^2/s$ where h is the height of the caudal fin and s is the surface area of the caudal fin extending to the narrowest part of the caudal peduncle (Palomares and Pauly, 1998)

T' = mean annual temperature of the water body (1000/°Kelvin);

h and d refer to the type of food consumed, h= 1 for herbivores and 0 for all other groups, and d= 1 for detritivores and 0 for all other groups (Pitcher *et al.*, 2002; Palomares and Pauly, 1998). Consumption values for non-fish species were the same as those used in Heymans and Pitcher (2002).

3.2.4 Diet

Diet information was assumed to be similar to that used in the 1900 Back to the Future model (Heymans and Pitcher, 2002). In most cases, this diet data was taken from Bundy *et al.* (2000), which calculated diet composition from available stomach contents from the time period of 1985-1987 or information obtained from the literature. As an approximation, the diet is assumed to be the same over the entire study area and was used for both models (See Appendix 1 for diet data).

3.2.5 Landings

Domestic and international landings information was compiled from ICNAF Statistical Bulletins for the years 1954-1960, beyond which, all fish landings data are included in the NAFO databases (www.nafo.ca). DFO publications (Canadian Stock Assessment Secretariat, Underwater World, etc.) were used to assemble landings for marine mammal species. All landings were converted to metric tonnes per kilometre squared per year and fit into Equation (1) as the term C_x, i.e., the catch for species/species group x (See Table 3.2 for landings data).

3.3 Balancing the Model

Parameters were entered into the Ecopath program, and the Basic Parametrization option was selected to run the model. When Basic Parameterization is chosen, Ecopath links the production of each species group with the consumption of all species groups and uses the linkages to estimate the missing parameters, that is, it solves for the unknowns in the system of linear equations (Christensen and Walters, 2000). The Basic Estimates window is the first look at the model. Ecotrophic efficiency is the primary check on the model and is flagged when it is equal to 0, or greater than 1 (Christensen and Walters, 2000). When $EE = 0$ this means that the species group is not being consumed by another species group within the model and it is not being exported (Christensen and Walters, 2000).

In the initial running of the mid-1950s model, walrus, ducks and planktivorous birds all were $EE = 0$, and remain unconsumed in the final version of the model. Walrus were not available to humans in the early 1950s, and the diet information available did not indicate any species consuming the seabird groups. We can be reasonably sure that there was some local consumption of seabird species by humans (mostly common murres) and some piscivorous seabirds were also used as bait in longline fisheries of the early twentieth century (Tasker *et al.*, 2000), so this estimate may not reflect the reality of the time. Mortality of birds away from colonies in general is less than 10% per year, based on breeding studies (Schneider, *pers.comm.* 2004). The biomass of birds is relatively small when held up against many of the fish species within the model, i.e., not

accounting for a small amount of local seabird landings would make very little difference to the model as a whole.

An $EE > 1$ is a larger problem; it means that more of that species or species group is being consumed or caught than is being produced in the current model scenario (Christensen and Walters, 2000). In this case, input data have to be re-examined, normally starting with the diet information and production estimates. Gross conversion efficiency (*GE*), i.e., the ratio between production and consumption, is another useful parameter to check when balancing a model. This ratio is limited by the physiology of the species and should be between 0.1 and 0.3 for most groups except for those that grow quickly such as microbes. Most species consume 3-10 times what they produce (Christensen and Walters, 2000). The best practice is to make a single change at a time, record the change, then rerun the model until inconsistencies are reduced to a minimum. Generally, the modeller should remember which of the data are the most reliable and avoid changing these. There is really no one way to balance a model in Ecopath, though it is recommended that the user start with the largest discrepancy as this often helps to balance some other species. In addition, an inaccurate, yet balanced model is of limited utility; the modeller's goal should not necessarily be to balance, but to fill a model with the best possible data. It is also advisable to identify key, or base groups at each trophic level that are changed as little as possible (assuming knowledge of these groups is good).

3.3.1 Balancing the mid-1950s Model

Fortunately, both models were relatively easy to balance; in both cases, addressing the largest discrepancy solved smaller imbalances. In the mid-1950s model; the ecotrophic efficiency term for harp seals was 2.172, that is, there were over twice as many harp seals being caught than were being produced according to the original estimates. The biomass estimate entered was a little low, at $0.300 t \cdot km^{-2}$. If we had allowed Ecopath to estimate biomass by entering 0.95 EE, the resulting biomass was higher than that used in the 1900 model; this indicates that a low biomass was not the main source of the problem. Modifying the diet proportions of harp seals produced far more problem in the balancing of its prey species. Instead, the *P/B* value was examined. *P/B* (=*Z* (total mortality)) in the models for 1900 and the 1980s were calculated as $0.102 \cdot year^{-1}$ (Bundy *et al.*, 2000). Stenson *et al.* (1999), suggest that the natural mortality rate of harp seals is $0.085 \cdot year^{-1}$, updating values from Shelton *et al.* (1996); adding this to the fishing mortality rate obtained in the mid-1950s model, resulted in a total mortality that is slightly higher at $0.155 \cdot year^{-1}$. When this value was plugged into the model along with a biomass estimate slightly higher than the original value, or $0.45 t \cdot km^{-2}$, harp seals balanced. Trites *et al.* (1999), had a similar problem balancing a marine mammal group in their model of the Bering Sea, though in that case they reduced the harvest value. The landings of harp seals in the mid-1950s model are a quantity that I am more certain of than any guesstimate of biomass, and therefore the harvest values were left as they were.

3.3.2 Balancing the late-1960s Model

Both adult and juvenile cod were unbalanced in the initial run of the late-1960s model. Originally, we assumed that the biomass of cod in the 1960s would have been reduced substantially when compared with the mid-1950s model, and the estimates were a bit too low, but as with harp seals in the mid-1950s model, there were apparent problems with the production term. If P/B is equal to the total mortality for adult cod, and fishing mortality was higher than it had been in 1900, it would be logical that the P/B used should be closer to that of the 1980s. Summing estimates of fishing mortality from 1968-70 and natural mortality (Heymans and Pitcher, 2002), indicated a P/B near $0.3 \cdot year^{-1}$. Trying that P/B and setting EE=0.95, brought the biomass up nearer to that estimated in the mid-1950s model. Keeping P/B = $0.3 \cdot year^{-1}$ and a biomass of $6.5 t \cdot km^{-2}$, balanced adult cod. Juvenile cod biomass was increased to $0.9 t \cdot km^{-2}$, slightly less than the proportion suggested in the previous section. The total mortality (z) of juvenile cod is likely higher than the value included as P/B in both models as estimates of natural mortality for juvenile cod are typically near $0.2 \cdot yr^{-1}$ (Campana *et al.*, 1989 and Svåsand and Kristiansen, 1990) and fishing mortality is certainly a factor as the 'juvenile' cod group include fish as large as 35cm. A study of mortality of coastal cod in Norway estimated total mortality (z) to be as high 1.05 in juvenile cod in their third year of life (Julliard *et al*, 2001).

In balancing adult cod the skates shifted out of balance, though this was easily remedied by increasing the skate biomass estimate from 0.27t·km^{-2} to 0.275t·km^{-2}, which fits the trend presented in the previous section.

Harp seals, as in the mid-1950s model were not balanced (EE= 1.951) in the initial run of the late 1960s model. They were balanced by raising the P/B to 0.155, and by increasing biomass to 0.350t·km^{-2}.

After balancing the models, all P/Bs were checked to see how well they matched the sum of fishing mortality and natural mortality obtained from Fishbase (Froese and Pauly, 2002). Non-fish species like marine mammal species P/B values were double-checked in related literature. It is reasonable to assume that, as with Atlantic cod, if fishing mortality increased, the P/B ratios might have to be adjusted slightly to account for more than natural mortality in addition to fishing mortality losses.

Table 3.1: Species and species groups used in Ecopath models of the Newfoundland and Labrador Shelf

	Ecopath Group	Species
1	Walrus	*Odobenus rosmarus*
2	Cetaceans	Humpback Whale (*Megaptera novaeangliae*), fin whale (*Balaenoptera physalus*), minke whale (*B. acutorostrata*), sei whale (*B. borealis*), blue whale (*B. musculus*), sperm whale (*Physeter catodon*), pilot whale (*Globicephala melaena*) and harbour porpoise (*Phocoena phocoena*)
3	Grey Seals	*Halichoerus grypus*
4	Harp Seals	*Phoca groenlandica*
5	Hooded Seals	*Cystophora cristata*
6	Ducks	Common eider (*Somateria mollissima*), scoters (*Melanitta sp.*) and oldsquaws (*Clangula hyemalis*)
7	Piscivorous Birds	Great auk (*Pinguinus impennis*), northern gannet (*Sula bassana*), great cormorants (*Phalacrocorax carbo*), double crested cormorant (*P. auritus*), herring gull (*Larus argentatus*), ring billed gull (*L. delawarensis*), common black headed gull (*L. ridibundus*), black-legged kittiwakes (*Rissa tridactyla*), common tern (*Sterna hirundo*), arctic tern (*S. paradisaea*), Caspian tern (*Sterna caspia*), common murre (*Uria aalga*), thick billed murre (*U. lomvia*), black guillemot (*Cepphus grylle*), razorbill (*Alca torda*), Atlantic puffins (*Fratercula arctica*), northern fulmar (*Fulmarus glacialis*), Manx shearwater (*Puffinus puffinus*), greater shearwater (*Puffinus gravis*) and sooty shearwater (*P. griseus*)
8	Planktivorous Birds	Leach's storm petrel (*Oceanodroma leucorhoa*) and dovekies (*Alle alle*)
9	Adult Cod > 40cm	*Gadus morhua*
10	Juvenile Cod < 40cm	
11	American plaice < 35cm	*Hippoglossoides platessoides*
12	American plaice > 35cm	
13	Greenland halibut < 40cm	*Reinhardtius hippoglossoides*
14	Greenland halibut > 40cm	
15	Yellowtail flounder	*Limanda ferruginea*
16	Witch flounder	*Glyptodelphalus cynoglossus*

17	Winter flounder	*Pseudopleuronectes americanus*
18	Skates	Barndoor (*Raja laevis*), thorny (*R. radiata*), smooth (*R. senta*), winter (*R. ocellata*) and little skate (*Leucoraja erinaceae*)
	Ecopath Group	Species
19	Dogfish	*Squalus acanthias*
20	Redfish	Deepwater redfish (*Sebastes mentella*) and Acadian redfish (*S. fasciatus*)
21	Transient Mackerel > 29cm	*Scomber scombrus*
22	Large Demersal piscivores > 40cm	White hake (*Urophycis tenuis*), silver hake (*Merluccius bilinearis*), monkfish (*Lophius americanus*), sea raven (*Hemitripterus americanus*), cusk (*Brosme brosme*) and Atlantic halibut (*Hippoglossus hippoglossus*)
23	Large Demersal piscivores < 40cm	
24	Large Demersal Feeders > 30cm	Haddock (*Melanogrammus aeglefinus*), longfin hake (*Phycis chesteri*), red hake (*Urophycis chuss*), wolffish (*Anarhichas* spp.), grenadiers (*Coryphaenoides* spp.), eelpouts (*Lycodes* spp.) and batfishes (Ogcocephalidae)
25	Other Large Demersals < 30cm	
26	Small Demersals.	Rocklings (*Enchelyopus* spp.), gunnel (*Pholis gunnelis*), alligator fishes (*Ulcina olriki*), Atlantic poachers (*Leptagonus decagonus*), snakeblennies (*Lumpenus lampretaeformis*), shannies (*Leptoclinus* spp.), sculpin (*Myoxocephalus* spp.), searobins (*Prionotus* spp.) and eelblennies (*Anisarchus* spp.)
27	Lumpfish	Lumpsuckers (*Cyclopterus lumpus*)
28	Greenland cod	*Gadus ogac*
29	Atlantic salmon	*Salmo salar*
30	Capelin	*Mallotus villosus*
31	Sandlance	*Ammodytes dubius*
32	Arctic cod	*Boreogadus saida*
33	Herring	*Clupea harengus harengus*
34	Transient pelagics	Bluefin tuna (*Thunnus thunnus*), swordfish (*Xiphias gladius*), porbeagle (*Lamna nasus*), basking shark (*Cetorhinus maximus*) and other sharks (Elasmobracchii)
35	Small pelagics	Shad (*Alosa sapidissima*), butterfish (*Peprilus triacanthus*), argentine (*Argentina silus*), juvenile mackerel (*Scomber scombrus*) and Atlantic rainbow smelt (*Osmerus mordax mordax*)
36	Small mesopelagics	Laternfishes (Myctophidae), pearlsides (*Maurolicus*

		muelleri) and barracudinas (*Paralepis elongata*)
37	Shortfin Squid	*Illex illecebrosus*
38	Arctic Squid	*Gonatus* spp.
39	Large Crabs > 95mm	Snow crab (*Chionocetes opilio*), jonah crab (*Cancer borealis*), red crabs (*Chaceon quinquedens*) and northern stone crabs (*Lithodes maia*)
	Ecopath Group	Species
40	Small Crabs < 95mm	Toad crabs (*Hyas areneus* and *H. coarctatus*), hermit crabs (*Pagurus* spp.), rock crabs (*Cancer irroratus*) and juveniles of large crabs
41	American lobster	*Homarus americanus*
42	Shrimps	Northern shrimp (*Pandalus borealis*) and deep water shrimp (*Pandalus montagui*)
43	Echinoderms	Sea urchin (*Strongylocentrus palliddus*), sand dollars (*Echinarachinus parma*) and others
44	Polychaetes	*Prionospio steenstrupi* and others
45	Bivalves	Sea scallops (*Placopecten magellanicus*), Icelandic scallops (*Chlamys islandicus*), propeller clams (*Cyrtodaria siliqua*), chalky macoma (*Macoma calcarea*) and others
46	Other benthic invertebrates	Brittlestar (*Ophiura sarsi*) and others
47	Large zooplankton	Euphasiids, Chaetognaths, hyperiid amphipods, Cnidarians, Ctenophores (jellyfish), mysids, tunicates >5mm and icthyoplankton
48	Small zooplankton	Copepods (*Calanus finmarchicus* and *Oithona similis*), tunicates <5mm and meroplankton
49	Phytoplankton	Diatoms and others
50	Detritus	

Table 3.2: Landings data entered (C_x) into models (International Commission for Northwest Atlantic Fisheries).

	Group Name	**Mid-1950s Model ($t \cdot km^{-2} \cdot year^{-1}$)**	**Late 1960s Model ($t \cdot km^{-2} \cdot year^{-1}$)**
2	Cetaceans	0.019	0.033
4	Harp seals	0.066	0.050
9	Atlantic cod > 40cm	1.2758	1.5971
11	American plaice > 35cm	0.0218	0.1646
13	Greenland halibut > 65cm	0.0010	0.0636
15	Yellowtail flounder		0.0374
16	Witch flounder	0.0060	0.0426
17	Winter flounder		0.0001
18	Skates	0.0001	0.0025
20	Redfish	0.0427	0.1024
21	Transient mackerel > 29cm	0.0004	0.0008
22	Large demersal piscivores > 40cm	0.0182	0.0037
24	Large demersal feeders > 30cm	0.2053	0.0409
29	Salmon	0.0015	0.0023
30	Capelin	0.0001	0.0047
33	Herring	0.0064	0.0067
34	Transient pelagics		0.0020
35	Small pelagics	0.0003	0.0002
37	Shortfin Squid		0.00001
39	Large crabs >95cm		0.0007
41	Lobster	0.0026	0.0012
45	Bivalves	0.0028	0.0001
	SUM	**1.670**	**2.4866**

Chapter 4: Results

The models indicate that the ecosystem on the Newfoundland and Labrador Shelf in 1968-70 was remarkably similar to that of 1954-56, despite intense fish harvesting during the fifteen intervening years. In this chapter I will describe changes observed between the two systems and how the input biomasses I calculated compare to trends originating from other models created by the Back to the Future research team, Heymans and Pitcher (2002) (See Tables 4.1 and 4.2 for balanced model parameters).

4.1.1 Biomasses

The graphs in Figure 4.1, illustrate the trends in biomass from 1450, 1900, 1985-87 and 1995-97, i.e., the models produced by Heymans and Pitcher (2002), with two data points added for the mid-1950s and late-1960s models. The data points for 1450 could not be easily illustrated on these graphs and as such the X axis has been cropped, but the line added shows the direction coming from the pre-European contact (1450) model. In most cases, the biomasses estimated by Ecopath for the mid-1950s and late-1960s models, fit well with the overall decline or increase suggested by the information provided by the 1900 and 1980s models. However, there are a few exceptions.

Figure 4.1:F illustrates the biomass trend for American plaice > 35cm. The biomass calculated by the mid-1950s model is along the downward trend assumed by noting the biomass estimates in the 1900 model and that for the mid-1980s model,

however there is a substantial increase in the estimate of biomass in the late-1960s model, before a decline into the mid-1980s. An increase in fishing mortality (See Table 4.4 and Figure 4.3) in the late-1960s model (very few landings were reported for them in the mid-1950s and far more in the late 1960s), would increase the demand on this group and hence Ecopath increased the biomass estimate.

Large demersal feeders >30cm, which includes species such as haddock, wolffish and the grenadiers, have a substantial increase in biomass between 1900 and 1954 (Figure 4.1:Q). The landings reported for this species group in the mid-1950s model are greater than the biomass calculated in the model of 1900.

There is also an unexpected trend in large crabs >95cm (4.1:AH), however in this case, the biomasses calculated by the models are quite a bit smaller than the biomasses estimated in 1900 and in the 1980s.

Overall, the biomass calculations add detail to the shape of species declines culminating in the low numbers observed in the mid-1980s. They suggest that for many species a sudden decline in stock size occurred during the 1970s and onwards rather than a continuous decline throughout the entire twentieth century. This pattern is suggested in Atlantic cod > 40cm, American plaice <35cm, dogfish, large demersal piscivores, small demersal feeders, sandlance, shortfin squid, Arctic squid, small crabs < 95cm, and shrimp.

Figures 4.2 and 4.3 illustrate the percent change in biomass for species groups between 1900 and the mid-1950s (4.2), and between the mid-1950s and late-1960s (4.3). According to these models, only one species group increased in biomass between 1900

and 1954. These are the large demersal feeders > 30cm. All other species groups showed a decline in biomass from 1900 to the late-1980s, ranging from –6% for the detritus group, to –95% for Greenland halibut <65cm. Between 1954 and 1970, there are six species groups whose biomasses increased: Greenland halibut >65cm, Greenland halibut <65cm, Transient mackerel >29cm, American plaice >35cm, Ducks and Atlantic salmon. The largest declines in this timeframe were in hooded seals, large demersal feeders >35cm and yellowtail flounder. Note that large demersal feeders <35cm had the largest percent increase in the previous time period.

4.1.2 Mortalities

There are several obvious changes in mortality between the mid-1950s model and the late-1960s model. Figure 4.4 exhibits the total mortality of the species groups divided into three mortality components: fishing mortality rate, predation mortality rate and other mortality. Predation mortality is the major component of the total mortality rate for most species groups (See also Tables 4.3 and 4.4). There is an increase in fishing mortality as a proportion of total mortality in cetaceans, American plaice >35cm and Greenland halibut >65cm and transient mackerel >29cm. There is a decrease in predation mortality as a proportion of the total for other mortality in Greenland halibut <65cm.

Taking a closer look at predation mortality, we can account for its distribution among all prey groups. Figure 4.5 displays the predation mortality distributed among most prey groups in 1954-1956 and 1968-1970. Total fishing mortality rate on all species

is included to see where it ranks among the species groups. In the mid-1950s model (1954-56), shrimp and small mesopelagics (including species such as lanternfishes, pearlsides and barracudinas) are the two most heavily preyed upon species groups. The total fishing mortality rate comes next, followed closely by predation mortality on sandlance. The species most preyed upon in the late-1960s model are virtually the same as the mid-1950s model. The fishery places second, behind only shrimp, in the late-1960s model, i.e., the total take of the fishery per year in 1968-1970 is greater than the predation mortality on all but one of the prey groups.

The fishery could certainly be considered a predator as it competes with natural predators in the ecosystem. In the mid-1950s model, the fishery places tenth, as most important consumer of prey behind species such as small crabs, harp seals and redfish (Figure 4.6). In the late-1960s model, the fishery moves up to fourth place as most significant predator behind small crabs, large demersal piscivores < 40cm (white hake, silver hake, cusk, Atlantic halibut, etc.) and small demersal feeders (juvenile haddock, wolffish and grenadiers). The order of predators below the most significant ones is much the same. When we look at the distribution of predation on vertebrate prey, as suggested by Bundy *et al.* (2000), the fishery is the fourth most significant predator in the system represented by the mid-1950s model (Figure 4.7). It is behind large demersal piscivores <40cm, harp seals and cetaceans. Harp seals and redfish are also important predators in this model. In the late-1960s model, large demersal piscivores < 40cm are again the top predator in terms of amount of consumption, and the fishery places second. Other predators have roughly the same role in each system. Note that the total fishing mortality

in this figure (4.7) is also only on vertebrate species; there would also be some landings on invertebrates such as squid and lobster which are omitted for consistency with vertebrate-only predators.

4.1.3 System Ratios

System ratios from Ecopath show that the mid-1950s model exceeds the late-1960s model in terms of total consumption, exports, respiratory flows and flows to detritus (Table 4.5). The mid-1950s model has a greater total system throughput than the late-1960s model. The mid-1950s model also has greater total production. The total catch in the late 1960s model, however, is 30% higher than that of the mid-1950s model.

As more countries expanded their fishing effort the catch began to diversify and include more pelagic species. The mean trophic level of the catch in the mid-1950s modelled system is the same as that in the late-1960s system, however gross efficiency, which represents fisheries catches relative to the total primary production in a system is also of interest. The gross efficiency of the late-1960s model far exceeds that of the mid-1950s model, again pointing toward a trend in harvesting species lower in the trophic food web rather than on apex predators. The weighted average for this parameter for all fisheries globally (in the late 20^{th} century) is 0.0002 (Christensen and Walters, 2000).

Two ratios considered to be indices of the stage of development and link to the extent of 'fishing down', are inconsistent between models; they are the calculated total primary production over total respiration and over total biomass. The late-1960s model

slightly exceeds the mid-1950s model in total primary production over total respiration. Production would be expected to exceed respiration in the early stages of development in a system, and hence the ratio would be greater than 1. The late-1960s model also slightly exceeds the mid-1950s model in the total primary production over total biomass ratio. In this case, the ratio suggests that the latter system would have slightly less accumulated biomass and would be farther 'ahead' in its stage of development. (Christensen and Walters, 2000). Overall, these differences are so slight and due to uncertain input parameters, it may be more appropriate to state that these ratios are the same between models.

Net system production is another index that differs between the two models. The net system production is the difference between total primary production and total respiration. This measure should be large in systems which have sustained little harvesting and are not considered to have been 'fished down.' This value is large in both the mid-1950s and late-1960s models, but larger in the mid-1950s when compared with the late-1960s, suggesting it has been subject to less fishing pressure than the system represented by the late-1960s model, a result consistent with the fishery history.

The systems characterized by the mid-1950s and late-1960s models are equal in terms of other summary indices. They have equal ratios of total biomass over total throughput and they are equal in a term called the Connectance Index, which is the ratio of the actual number of links in the food web to the possible number (Christensen and Walters, 2000). The System Omnivory Index is also nearly equal (0.130 and 0.131). This index is a measure of the way in which the feeding interactions in the system are

distributed between the trophic levels. These to indices would provide more information if separate diet data had been provided for the two models.

4.2 Boxes and Trophic Flows

Ecosystem flows between species groups as predators and prey and between trophic levels can be expressed in different ways. One such method is a flow diagram, which places species groups in boxes organized by trophic level, whereby a box can be selected to illustrate the flow of energy. With fifty species groups, it would be impossible to illustrate all of the flows coming from and leading to all boxes in the models, however it can be useful to depict the role of one or two key species. Figure 4.8 represents the mid-1950s model and the role of Atlantic cod < 40cm (juvenile cod). Lines exiting the top of the box represent flows from predators while lines exiting the bottom represent flows to prey. These flow diagrams also depict flows out of boxes representing fishery catches, cannibalism and respiration. Figure 4.9 is another representation of the mid-1950s model, though this time the role of capelin is highlighted. In this case, nearly every species group at a trophic level above that estimated for capelin has a flow to the capelin box, indicating its role as a central prey species. The faded dashed lines are the role of juvenile cod illustrated in the previous figure. The position of the boxes on the X axis is an arbitrary placement to make all the boxes independent of each other, it is the position on the Y axis that indicates the trophic position of the species groups. These diagrams do

appear jumbled as 50 species groups are included; see Trites *et al.* (1999) for a simpler version in a reduced model of the Bering Sea.

Figure 4.10a is another way of looking at the distribution of trophic levels in the landings. It illustrates the landings by trophic level as a percent of the total landings, comparing the mid-1950s and late-1960s models. Trophic levels were split in half to allow for a more detailed analysis. Nearly all of the landings in both models are from species with trophic level 3.5- 3.99. The landings in the mid-1950s model actually include more at lower trophic levels than the late-1960s model.

Finally, it seemed logical to take a look at the biomass of the systems arranged into trophic pyramids. Figure 4.10b compares the biomass of systems represented by the mid-1950s and late-1960s models by trophic level. As with the catch figure, the biomass in each trophic level is considered as a percent of the biomass of the entire system. Not surprisingly, considering the results in the system ratios, the mid-1950s and late-1960s models are similar in terms of their trophic breakdown.

Table 4.1: Balanced Model Parameters for the mid-1950s model.

	Group Name	Biomass ($t \cdot km^{-2}$)	Production/ Biomass($year^{-1}$)	Consumption/ Biomass($year^{-1}$)	Ecotrophic Efficiency
1	Walrus	0.000001	0.060	16.846	0.000
2	Cetaceans	0.350	0.100	11.790	0.530
3	Grey Seals	0.000001	0.060	15.000	0.281
4	Harp Seals	0.450	0.155	17.412	0.953
5	Hooded Seals	0.065	0.109	13.100	0.000
6	Ducks	0.0002	0.250	54.750	0.000
7	Piscivorous Birds	0.010	0.250	54.750	0.313
8	Planktivorous Birds	0.003	0.250	54.750	0.000
9	Atlantic Cod > 40cm	8.162	0.198	1.091	0.831
10	Atlantic Cod < 40cm	1.360	0.155	1.637	0.676
11	American Plaice > 35cm	2.363	0.083	1.698	0.950
12	American Plaice < 35cm	11.476	0.124	2.547	0.950
13	Greenland Halibut > 65cm	0.0.61	0.165	1.193	0.950
14	Greenland Halibut < 65cm	0.014	0.455	1.789	0.950
15	Yellowtail Flounder	1.921	0.317	3.271	0.950
16	Witch Flounder	5.842	0.235	2.304	0.950
17	Winter Flounder	0.123	0.267	1.644	0.950
18	Skates	0.320	0.233	1.779	0.916
19	Dogfish	0.055	0.159	2.210	0.950
20	Redfish	14.034	0.113	1.702	0.950
21	Transient Mackerel > 29cm	0.001	0.530	5.940	0.950
22	Large Demersal Piscivores > 40cm	1.122	0.098	1.107	0.950
23	Large Demersal Piscivores < 40cm	15.324	0.147	1.660	0.950
24	Large Demersal Feeders > 30cm	2.799	0.155	1.386	0.950
25	Small Demersal Feeders	16.014	0.232	2.079	0.950
26	Other Small Demersals	6.302	0.564	4.474	0.950
27	Lumpfish	0.413	0.114	1.374	0.950
28	Greenland Cod	0.416	0.101	1.265	0.950
29	Salmon	0.025	0.279	4.093	0.950

30	Capelin	14.000	0.578	4.900	0.712
31	Sandlance*	18.320	0.981	4.904	0.950
32	Arctic Cod	6.960	0.573	3.601	0.950
33	Herring	4.540	0.510	4.131	0.950
34	Transient Pelagics	0.071	0.183	1.999	0.950
35	Small Pelagics	1.492	0.638	5.291	0.950
36	Small Mesopelagics	7.374	1.422	4.789	0.950
37	Shortfin Squid*	2.503	0.600	4.000	0.950
38	Arctic Squid*	6.343	0.500	3.333	0.950
39	Large Crabs > 95cm	0.049	0.380	4.420	0.950
40	Small Crabs < 95cm	22.596	0.380	4.420	0.950
41	Lobster	0.014	0.380	4.420	0.950
42	Shrimp	11.578	1.450	9.670	0.950
43	Echinoderms	49.861	0.600	6.670	0.950
44	Polychaetes	20.094	2.000	6.330	0.950
45	Bivalves	54.699	0.570	22.220	0.950
46	Other Benthic Invertebrates*	23.087	2.500	12.500	0.950
47	Large Zooplankton*	73.381	3.433	13.732	0.950
48	Small Zooplankton*	84.229	8.400	28.000	0.950
49	Phytoplankton	58.878	93.100	-	0.500
50	Detritus	512.860	-	-	0.531

* Sandlance, Shortfin Squid and Arctic Squid had estimates of Production/Comsumption rather than P/B or Q/B; they were, 0.200, 0.150, and 0.150 respectively. There were similar values entered for Groups 46 (0.200) , 47 (0.250), and 48 (0.300).

Table 4.2: Balanced Model Parameters for late-1960s model.

	Group Name	Biomass ($t \cdot km^{-2}$)	Production/ Biomass($year^{-1}$)	Consumption/ Biomass($year^{-1}$)	Ecotrophic Efficiency
1	Walrus	0.000001	0.060	16.846	0.000
2	Cetaceans	0.350	0.100	11.790	0.952
3	Grey Seals	0.00001	0.060	15.000	0.281
4	Harp Seals	0.350	0.155	17.412	0.922
5	Hooded Seals	0.040	0.109	13.100	0.000
6	Ducks	0.0002	0.250	54.750	0.000
7	Piscivorous Birds	0.010	0.250	54.750	0.244
8	Planktivorous Birds	0.002	0.250	54.750	0.000
9	Atlantic Cod > 40cm	6.500	0.300	1.091	0.844
10	Atlantic Cod < 40cm	0.900	0.155	1.637	0.919
11	American Plaice > 35cm	3.710	0.083	1.698	0.950
12	American Plaice < 35cm	9.968	0.124	2.547	0.950
13	Greenland Halibut > 65cm	0.450	0.165	1.193	0.945
14	Greenland Halibut < 65cm	0.450	0.455	1.789	0.031
15	Yellowtail Flounder	1.791	0.317	3.271	0.950
16	Witch Flounder	4.671	0.235	2.304	0.950
17	Winter Flounder	0.077	0.267	1.644	0.950
18	Skates	0.275	0.233	1.779	0.990
19	Dogfish	0.055	0.159	2.210	0.950
20	Redfish	11.459	0.133	1.702	0.950
21	Transient Mackerel > 29cm	0.002	0.530	5.940	0.950
22	Large Demersal Piscivores > 40cm	0.966	0.098	1.107	0.950
23	Large Demersal Piscivores < 40cm	13.805	0.147	1.660	0.950
24	Large Demersal Feeders > 30cm	1.480	0.155	1.386	0.950
25	Small Demersal Feeders	14.214	0.232	2.079	0.950
26	Other Small Demersals	5.495	0.564	4.474	0.950
27	Lumpfish	0.396	0.114	1.374	0.950
28	Greenland Cod	0.360	0.101	1.265	0.950
29	Salmon	0.027	0.279	4.093	0.950
30	Capelin	13.500	0.578	4.900	0.774

31	Sandlance*	16.356	0.981	4.904	0.950
32	Arctic Cod	5.924	0.573	3.601	0.950
33	Herring	3.929	0.510	4.131	0.950
34	Transient Pelagics	0.057	0.183	1.999	0.950
35	Small Pelagics	1.349	0.638	5.291	0.950
36	Small Mesopelagics	6.145	1.422	4.789	0.950
37	Shortfin Squid*	2.186	0.600	4.000	0.950
38	Arctic Squid*	5.486	0.500	3.333	0.950
39	Large Crabs > 95cm	0.040	0.380	4.420	0.950
40	Small Crabs < 95cm	19.856	0.380	4.420	0.950
41	Lobster	0.009	0.380	4.420	0.950
42	Shrimp	9.962	1.450	9.670	0.950
43	Echinoderms	45.069	0.600	6.670	0.950
44	Polychaetes	17.258	2.000	6.330	0.950
45	Bivalves	48/298	0.570	22.220	0.950
46	Other Benthic Invertebrates*	20.100	2.500	12.500	0.950
47	Large Zooplankton*	64.722	3.433	13.732	0.950
48	Small Zooplankton*	74.492	8.400	28.000	0.950
49	Phytoplankton	52.048	93.100	-	0.500
50	Detritus	446.680	-	-	0.530

* Sandlance, Shortfin Squid and Arctic Squid had estimates of Production/Comsumption rather than P/B or Q/B; they were, 0.200, 0.150, and 0.150 respectively. There were similar values entered for Groups 46 (0.200) , 47 (0.250), and 48 (0.300).

Table 4.3: Mortality Coefficients for Mid-1950s Model.

	Group Name	Production/ Biomass (P/B=Z)	Fishing Mortality Rate	Predation Mortality Rate	Other Mortality
1	Walrus	0.06	0	0	0.06
2	Cetaceans	0.10	0.053	0	0.047
3	Grey Seals	0.06	0	0.017	0.043
4	Harp Seals	0.155	0.148	0	0.007
5	Hooded Seals	0.109	0	0	0.109
6	Ducks	0.25	0	0	0.25
7	Piscivorous Birds	0.25	0	0.078	0.172
8	Planktivorous Birds	0.25	0	0	0.25
9	Atlantic Cod > 40cm	0.198	0.156	0.008	0.033
10	Atlantic Cod < 40cm	0.155	0	0.105	0.050
11	American Plaice > 35cm	0.083	0.009	0.070	0.004
12	American Plaice < 35cm	0.124	0	0.118	0.006
13	Greenland Halibut > 65cm	0.165	0.015	0.141	0.008
14	Greenland Halibut < 65cm	0.455	0	0.432	0.023
15	Yellowtail Flounder	0.317	0	0.301	0.016
16	Witch Flounder	0.235	0.001	0.222	0.012
17	Winter Flounder	0.267	0	0.254	0.013
18	Skates	0.233	0	0.213	0.019
19	Dogfish	0.159	0	0.151	0.008
20	Redfish	0.113	0.003	0.104	0.006
21	Transient Mackerel > 29cm	0.53	0.288	0.216	0.027
22	Large Demersal Piscivores > 40cm	0.098	0.016	0.077	0.005
23	Large Demersal Piscivores < 40cm	0.147	0	0.140	0.007
24	Large Demersal Feeders > 30cm	0.155	0.073	0.074	0.008
25	Small Demersal Feeders	0.232	0	0.220	0.012
26	Other Small Demersals	0.564	0	0.536	0.028
27	Lumpfish	0.114	0	0.108	0.006
28	Greenland Cod	0.101	0	0.096	0.005
29	Salmon	0.279	0.061	0.204	0.014
30	Capelin	0.578	0	0.411	0.167

31	Sandlance	0.981	0	0.932	0.49
32	Arctic Cod	0.573	0	0.544	0.029
33	Herring	0.510	0	0.483	0.026
34	Transient Pelagics	0.183	0	0.172	0.009
35	Small Pelagics	0.638	0	0.606	0.032
36	Small Mesopelagics	1.422	0	1.351	0.071
37	Shortfin Squid	0.6	0	0.57	0.03
38	Arctic Squid	0.5	0	0.475	0.025
39	Large Crabs > 95cm	0.38	0	0.361	0.019
40	Small Crabs < 95cm	0.38	0	0.361	0.019
41	Lobster	0.38	0.181	0.180	0.019
42	Shrimp	1.45	0	1.378	0.072
43	Echinoderms	0.6	0	0.57	0.03
44	Polychaetes	2.00	0	1.9	0.1
45	Bivalves	0.57	0	0.541	0.029
46	Other Benthic Invertebrates	2.5	0	2.375	0.125
47	Large Zooplankton	3.433	0	3.261	0.172
48	Small Zooplankton	8.4	0	7.98	0.42
49	Phytoplankton	93.1	0	46.55	46.55
50	Detritus				

Table 4.4: Mortality Coefficients for Late-1960s Model.

	Group Name	Production/ Biomass (P/B=Z)	Fishing Mortality Rate	Predation Mortality Rate	Other Mortality
1	Walrus	0.06	0	0	0.06
2	Cetaceans	0.10	0.095	0	0.005
3	Grey Seals	0.06	0	0.017	0.043
4	Harp Seals	0.155	0.143	0	0.012
5	Hooded Seals	0.109	0	0	0.109
6	Ducks	0.25	0	0	0.25
7	Piscivorous Birds	0.25	0	0.061	0.189
8	Planktivorous Birds	0.25	0	0	0.25
9	Atlantic Cod > 40cm	0.300	0.246	0.008	0.047
10	Atlantic Cod < 40cm	0.155	0	0.142	0.013
11	American Plaice > 35cm	0.083	0.044	0.034	0.004
12	American Plaice < 35cm	0.124	0	0.118	0.006
13	Greenland Halibut > 65cm	0.165	0.141	0.015	0.009
14	Greenland Halibut < 65cm	0.455	0	0.012	0.443
15	Yellowtail Flounder	0.317	0.021	0.280	0.016
16	Witch Flounder	0.235	0.009	0.214	0.012
17	Winter Flounder	0.267	0.001	0.252	0.013
18	Skates	0.233	0.009	0.221	0.002
19	Dogfish	0.159	0	0.151	0.008
20	Redfish	0.133	0.009	0.117	0.007
21	Transient Mackerel > 29cm	0.53	0.370	0.169	0.027
22	Large Demersal Piscivores > 40cm	0.098	0.004	0.089	0.005
23	Large Demersal Piscivores < 40cm	0.147	0	0.140	0.007
24	Large Demersal Feeders > 30cm	0.155	0.028	0.144	0.009
25	Small Demersal Feeders	0.232	0	0.220	0.012
26	Other Small Demersals	0.564	0	0.536	0.028
27	Lumpfish	0.114	0	0.108	0.006
28	Greenland Cod	0.101	0	0.096	0.005
29	Salmon	0.279	0.082	0.184	0.014
30	Capelin	0.578	0	0.488	0.130

31	Sandlance	0.981	0	0.932	0.049
32	Arctic Cod	0.573	0	0.544	0.029
33	Herring	0.510	0.002	0.483	0.026
34	Transient Pelagics	0.183	0.035	0.139	0.009
35	Small Pelagics	0.638	0	0.606	0.032
36	Small Mesopelagics	1.422	0	1.351	0.071
37	Shortfin Squid	0.6	0	0.57	0.03
38	Arctic Squid	0.5	0	0.475	0.025
39	Large Crabs > 95cm	0.38	0.017	0.344	0.019
40	Small Crabs < 95cm	0.38	0	0.361	0.019
41	Lobster	0.38	0.131	0.230	0.019
42	Shrimp	1.45	0	1.378	0.072
43	Echinoderms	0.6	0	0.57	0.03
44	Polychaetes	2.00	0	1.9	0.1
45	Bivalves	0.57	0	0.541	0.029
46	Other Benthic Invertebrates	2.5	0	2.375	0.125
47	Large Zooplankton	3.433	0	3.261	0.172
48	Small Zooplankton	8.4	0	7.98	0.42
49	Phytoplankton	93.1	0	46.55	46.55
50	Detritus				

Table 4.5: Ecopath system statistics and ratios comparing the mid-1950s model and the late 1960s model. Higher values are highlighted in bold.

Parameter	Mid-1950s Model	Late 1960s Model
Sum of all consumption ($t \cdot km^{-2} \cdot year^{-1}$)	**6014.492**	5311.919
Sum of all exports ($t \cdot km^{-2} \cdot year^{-1}$)	**1879.693**	1664.405
Sum of all respiratory flows ($t \cdot km^{-2} \cdot year^{-1}$)	**3601.839**	3181.228
Sum of all flows to detritus ($t \cdot km^{-2} \cdot year^{-1}$)	**4006.358**	3540.392
Total System Throughput ($t \cdot km^{-2} \cdot year^{-1}$)	**15502**	13698
Sum of all production ($t \cdot km^{-2} \cdot year^{-1}$)	**6692**	5914
Mean trophic level of the catch	3.87	3.87
Gross efficiency (catch/net p.p)	0.000305	**0.00045**
Calculated total net primary production ($t \cdot km^{-2} \cdot year^{-1}$)	**5481.532**	4845.632
Total primary production/total respiration	1.522	**1.523**
Net system production ($t \cdot km^{-2} \cdot year^{-1}$)	**1879.693**	1664.405
Total primary production/total biomass	9.983	**10**
Total biomass/ total throughput	0.035	0.035
Total biomass (excluding detritus) ($t \cdot km^{-2}$)	**549.095**	484.578
Total catches ($t \cdot km^{-2} \cdot year^{-1}$)	1.67	**2.157**
Connectance index	0.231	0.231
System omnivory index	0.131	0.130

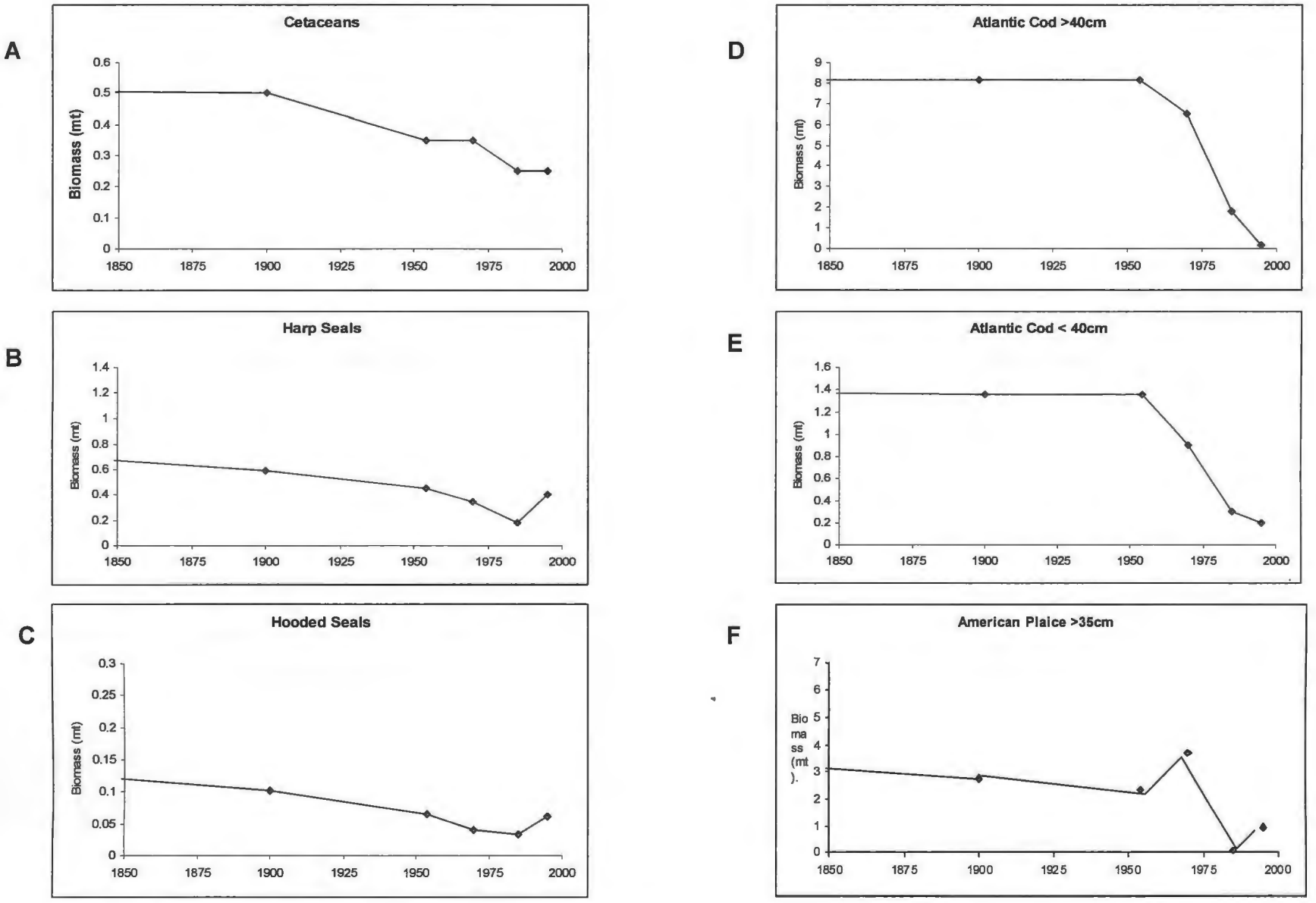
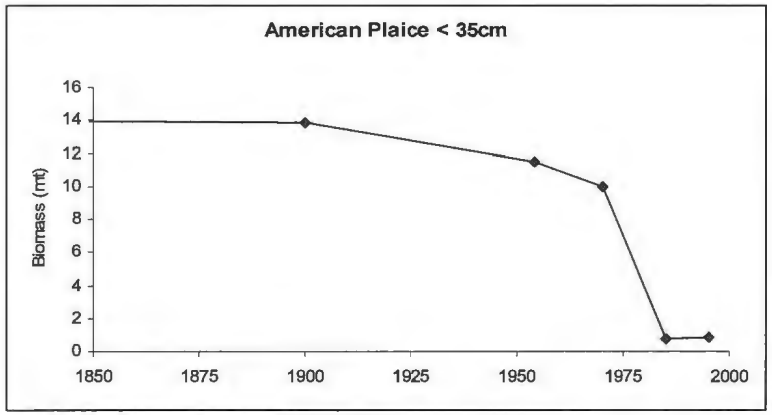


Figure 4.1: Biomass trends for most species groups A-AO (not included are Walrus and Grey seals- mainly extirpated in the area by the 1950s, and the three seabird groups- whose biomasses were not modified from the mid-1980s model).

G



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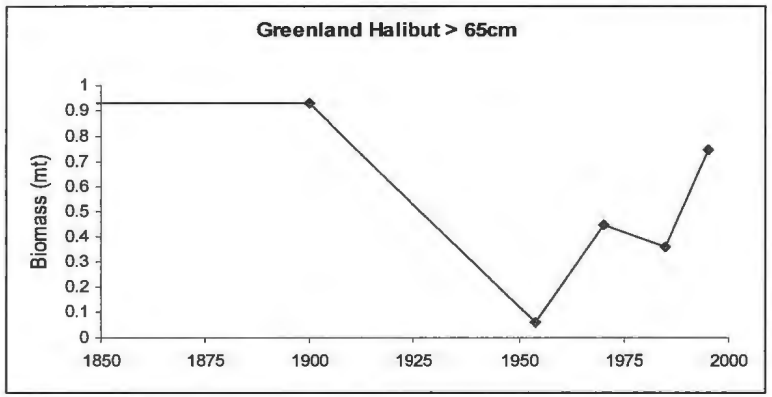

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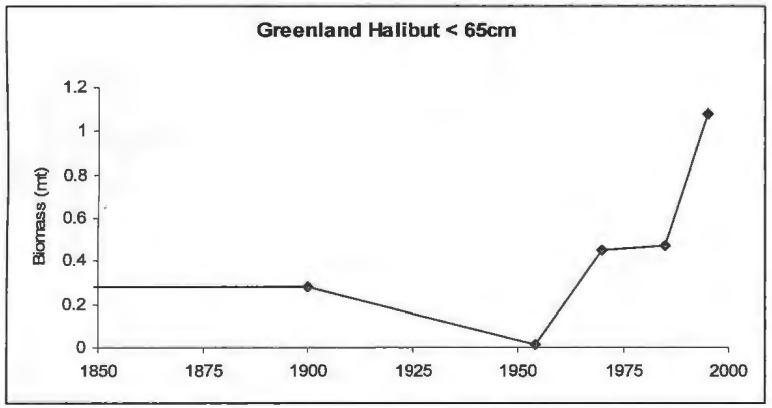

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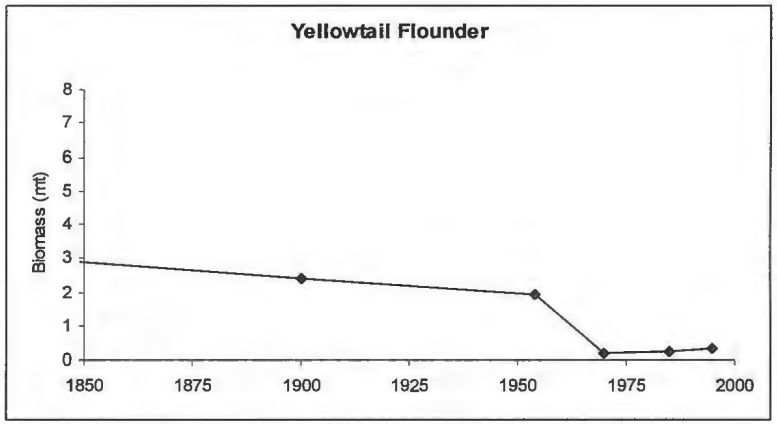

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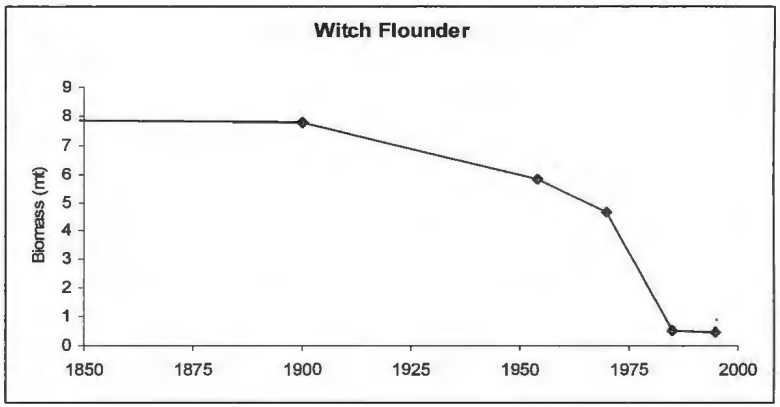

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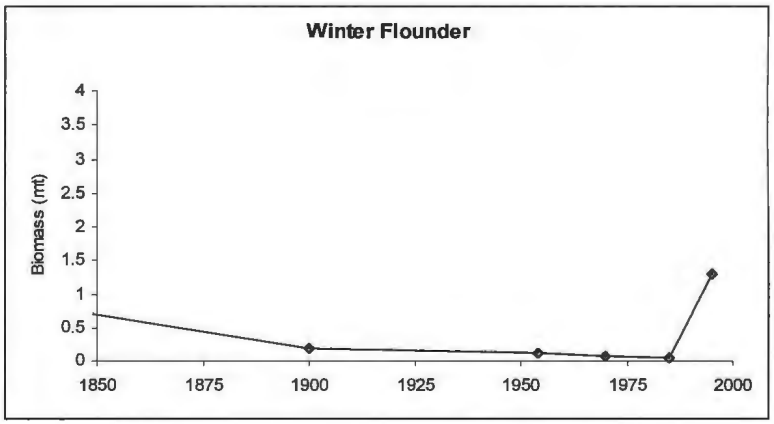

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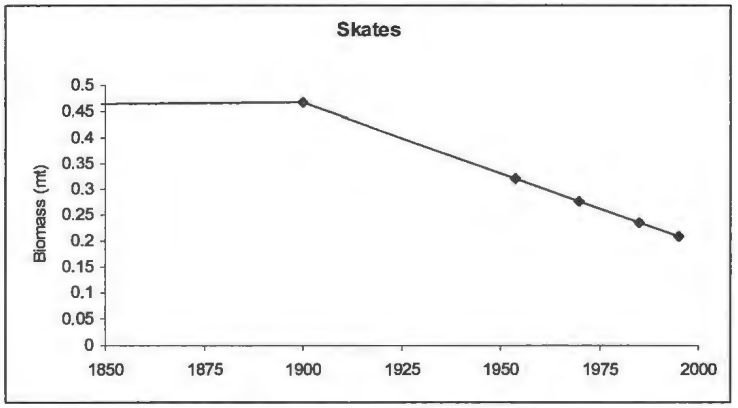

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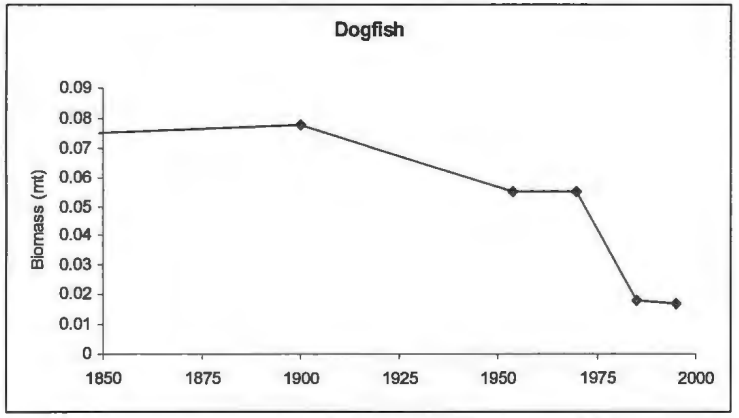

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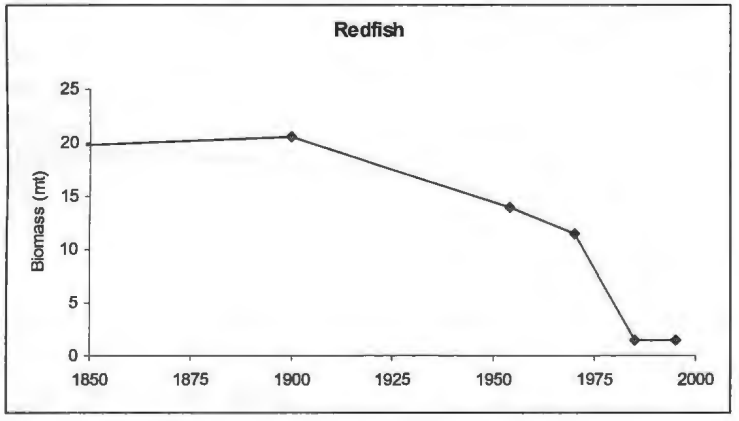

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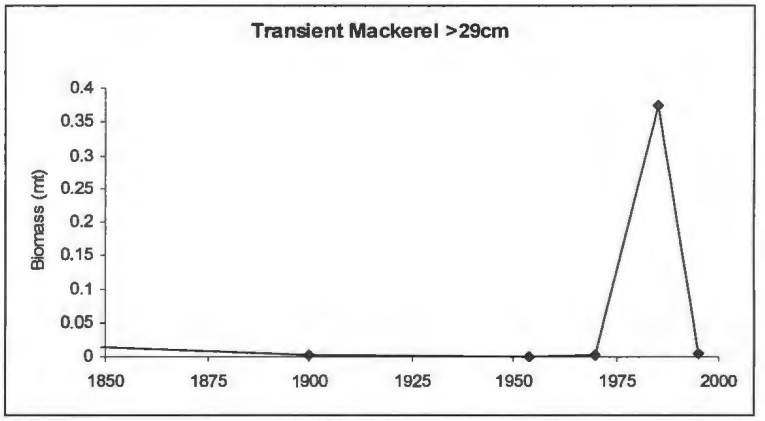

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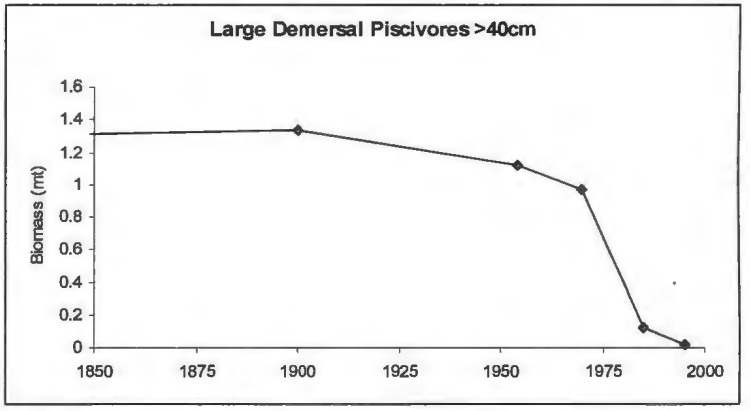

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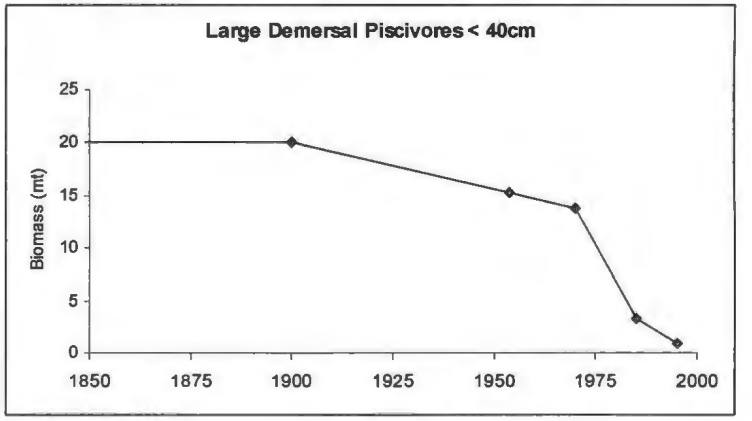

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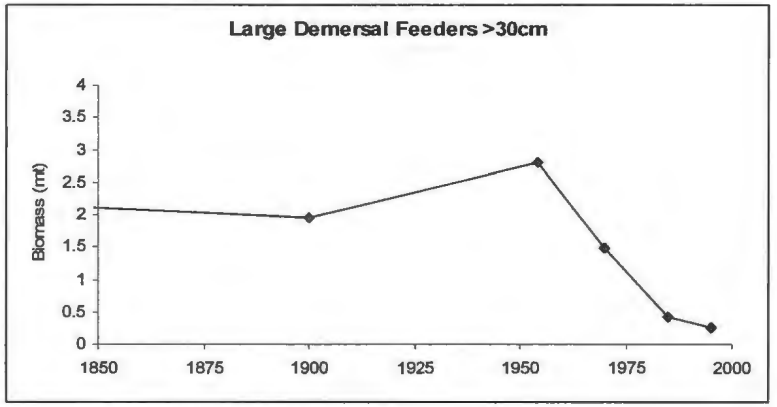

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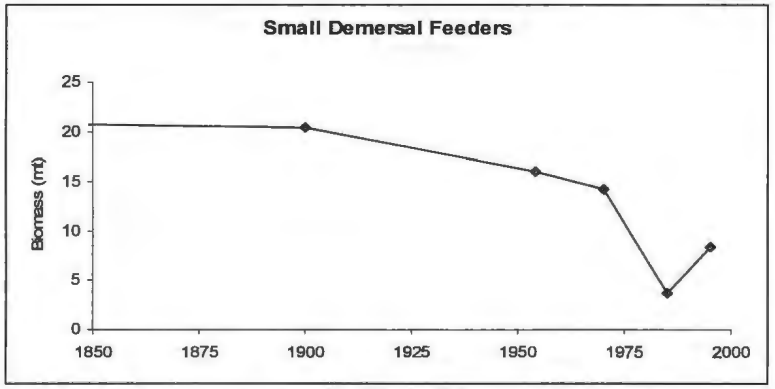

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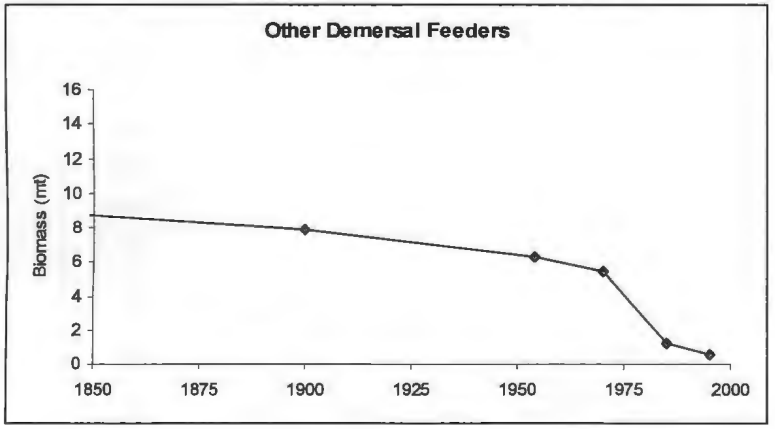

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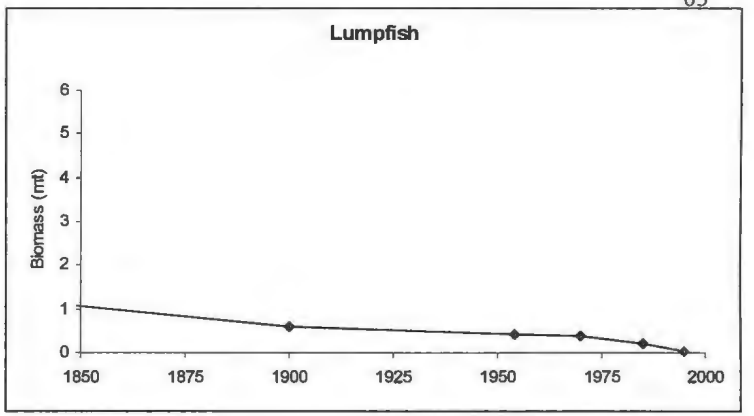

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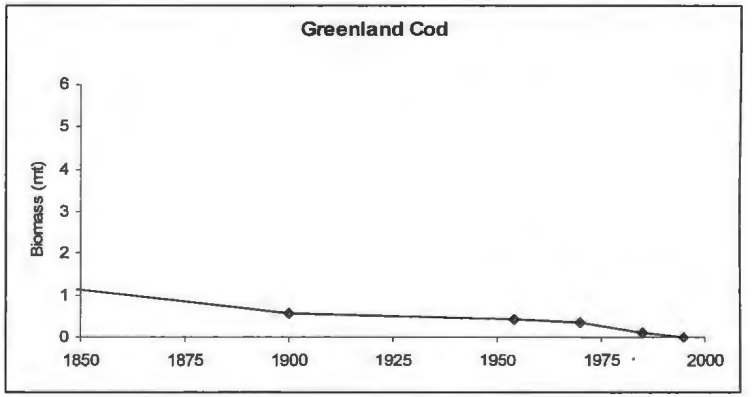

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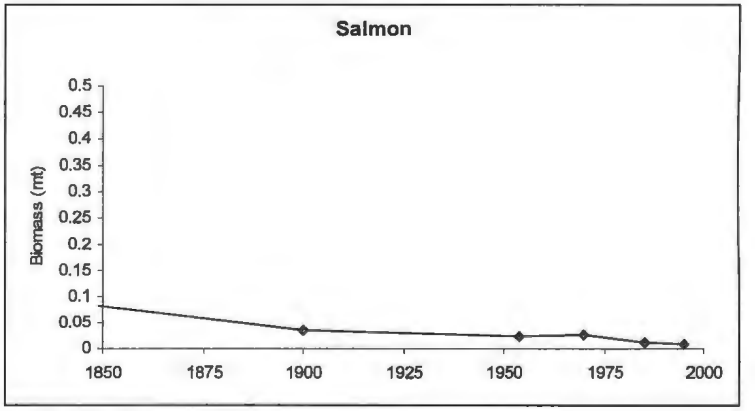

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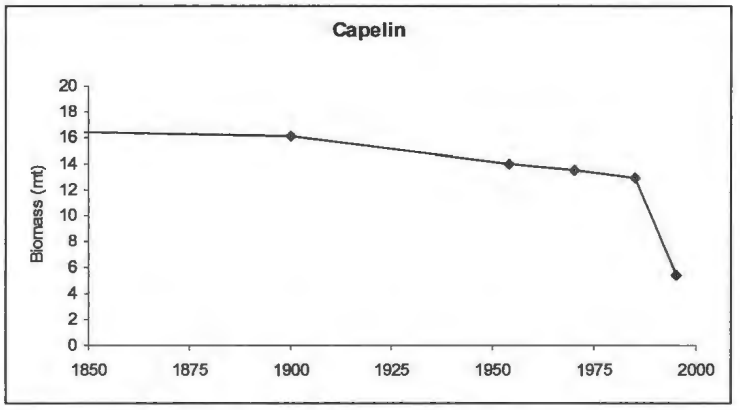

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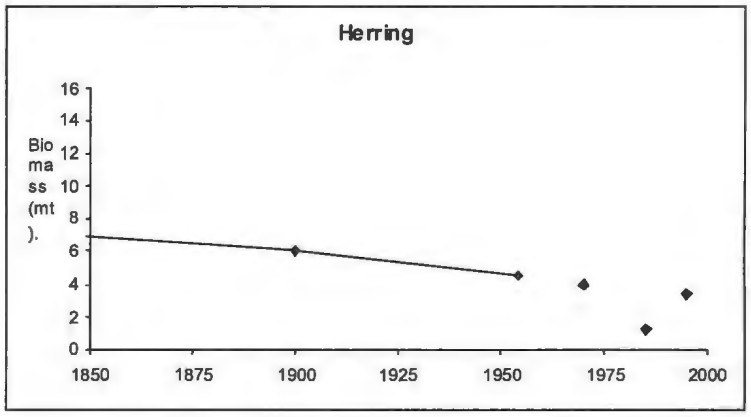

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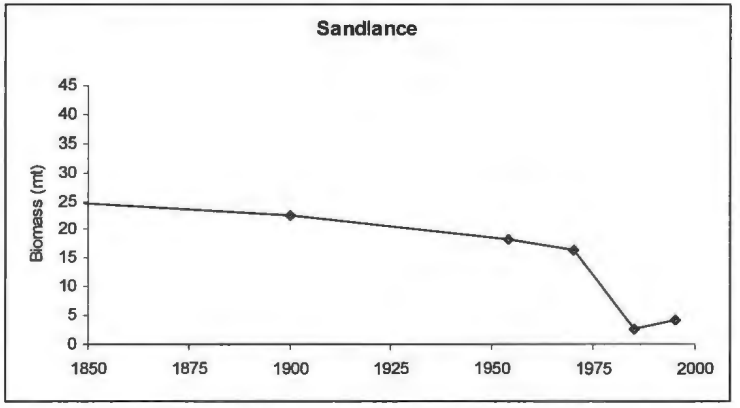

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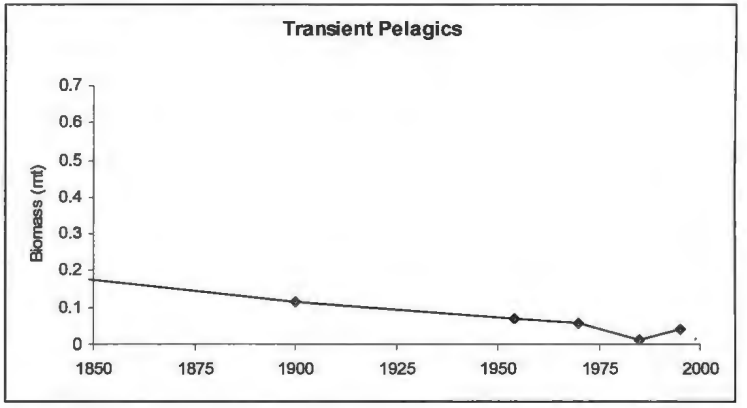

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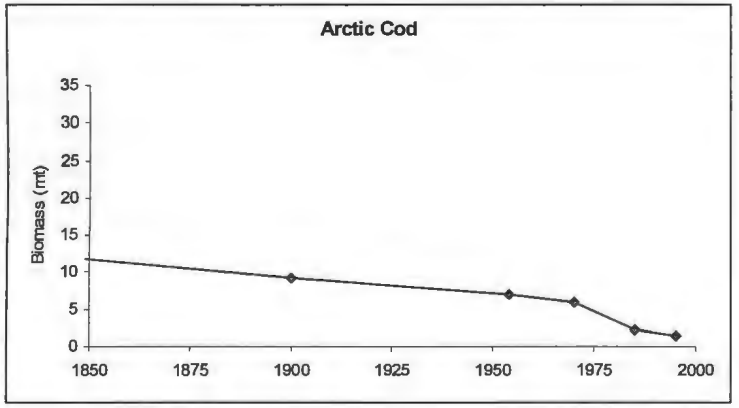

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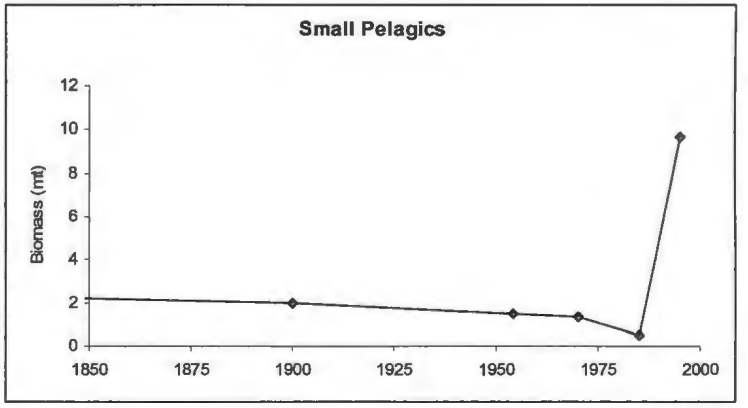

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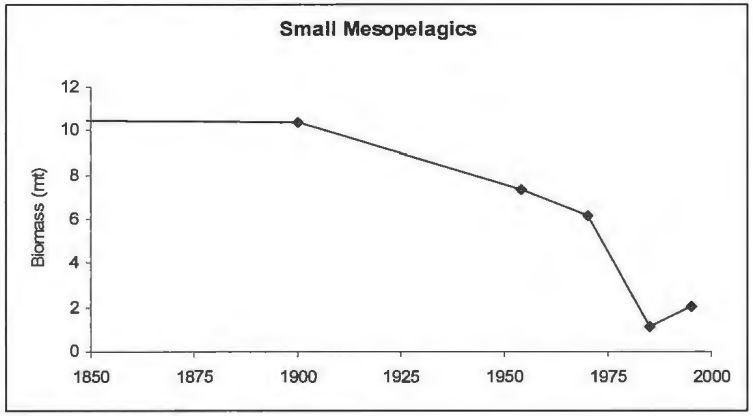

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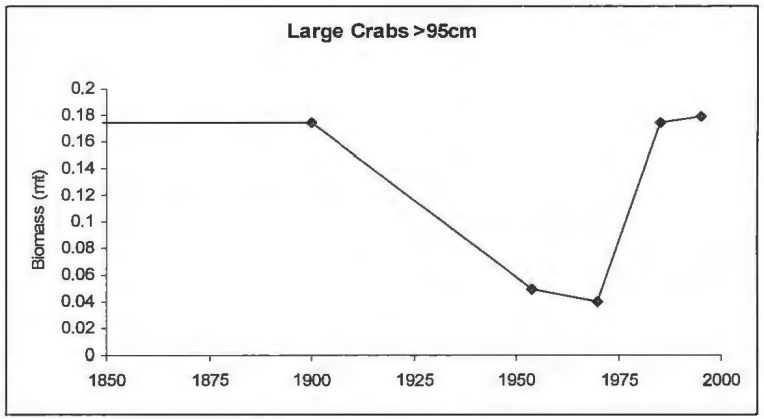

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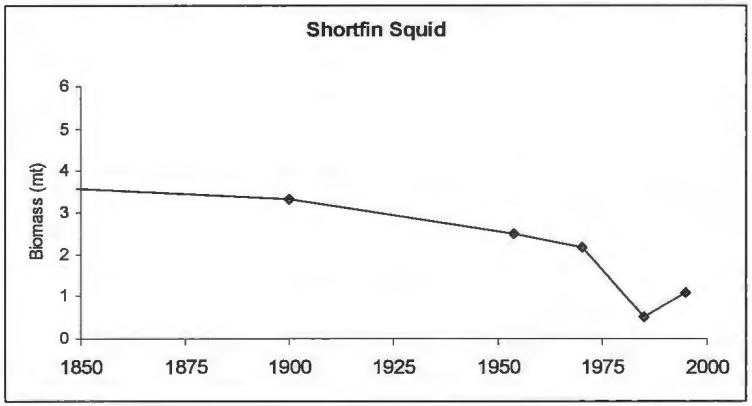

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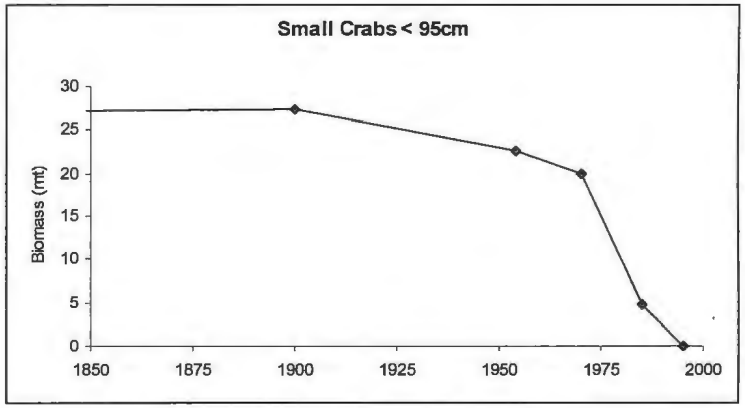

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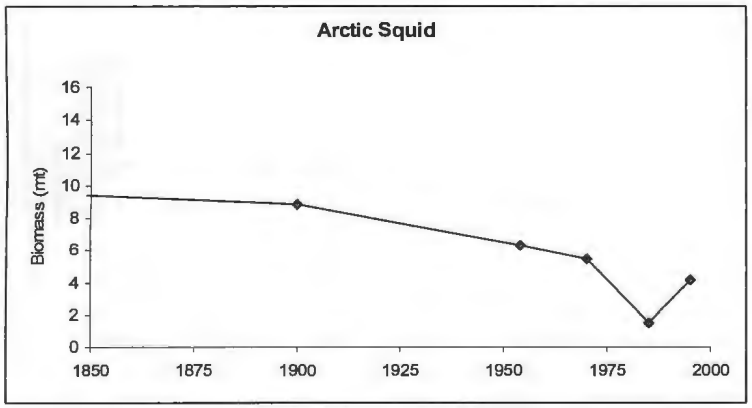

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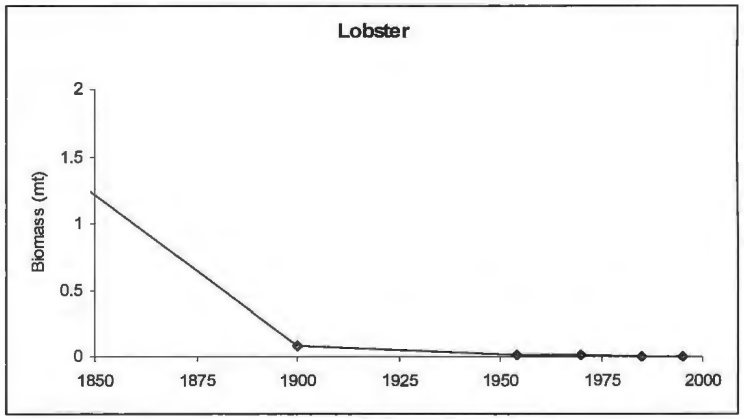

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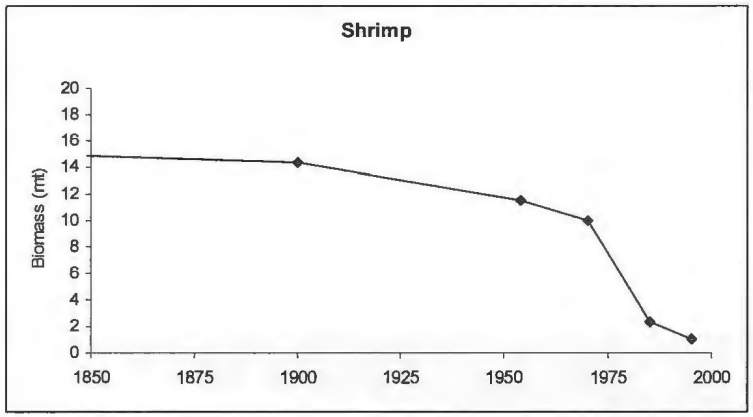

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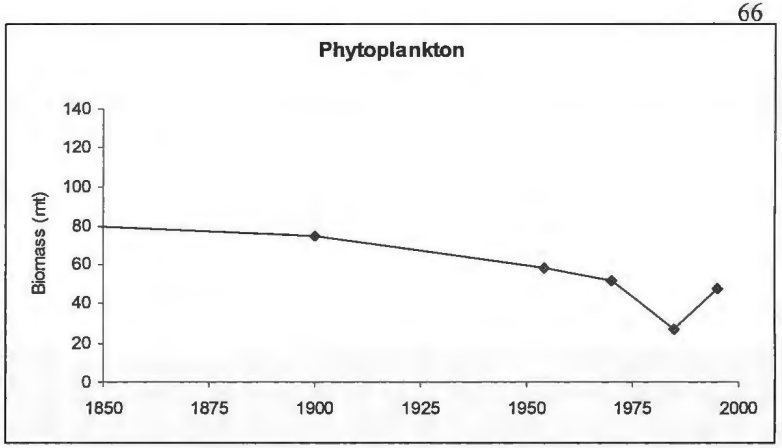

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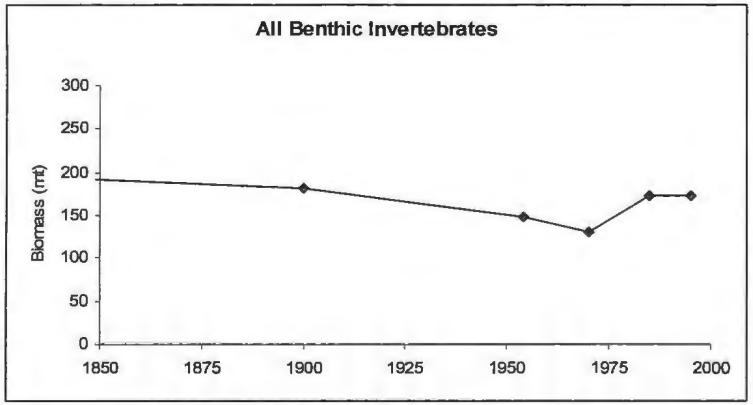

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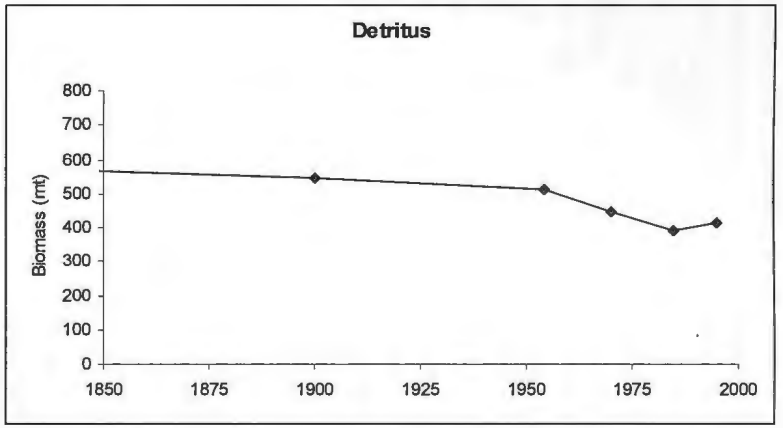

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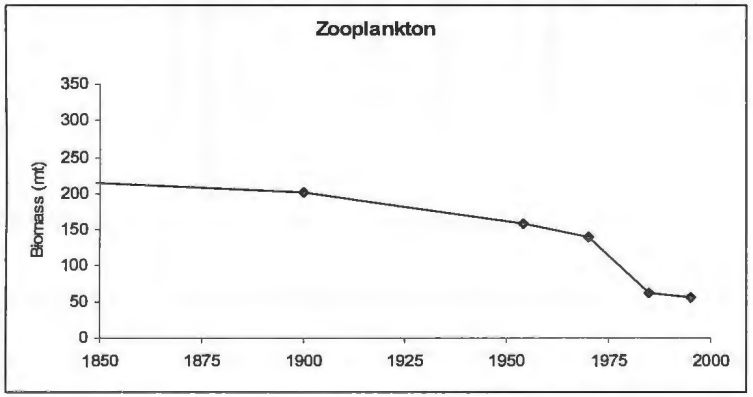


Figure 4.1: Continued (AL= Echinoderms, Polychaetes, Bivalves and Other Benthic Invertebrates, AM= Large Zooplankton and Small Zooplankton).

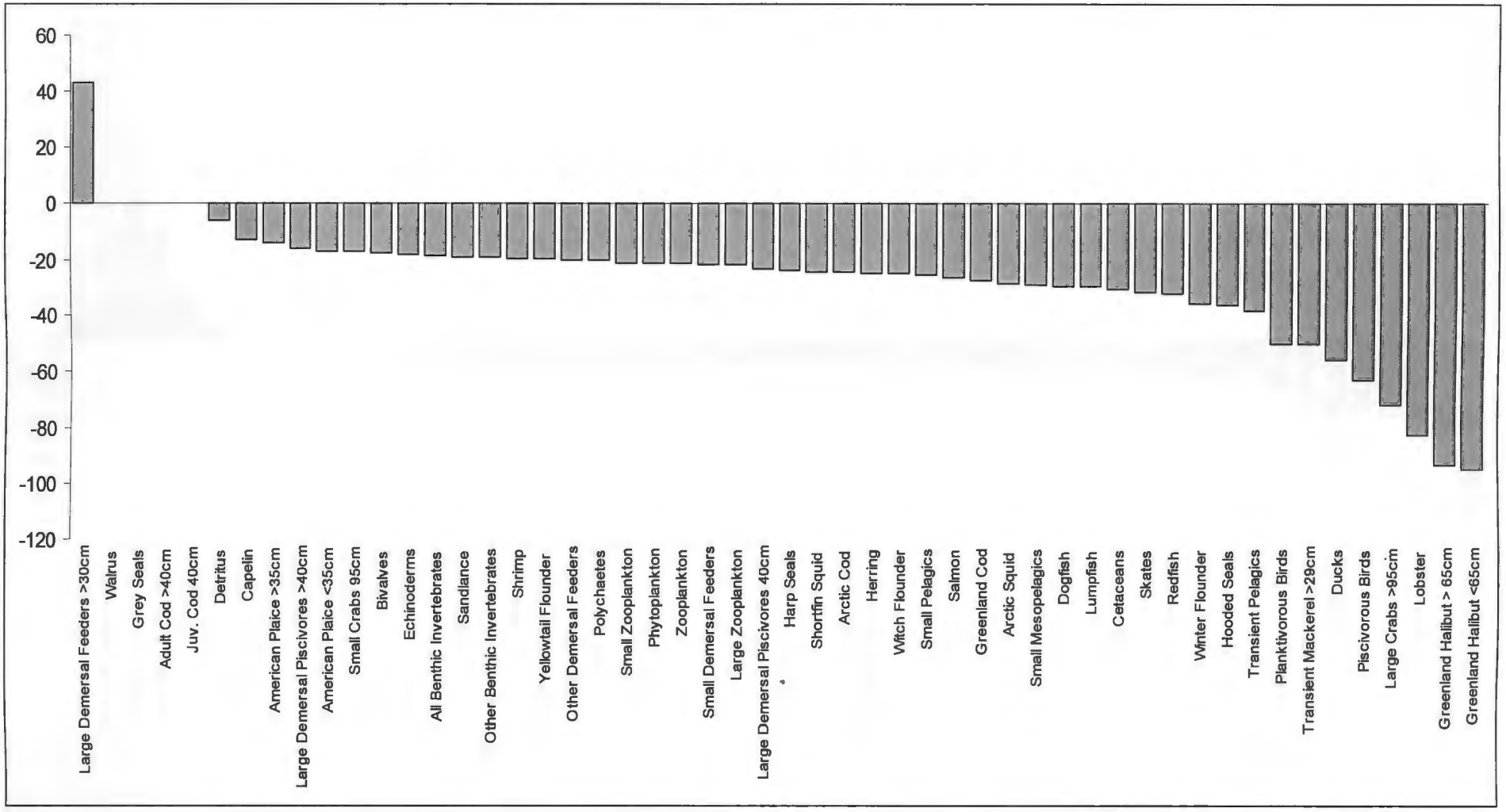


Figure 4.2: Percent Change in Biomass of species groups from 1900 to 1954.

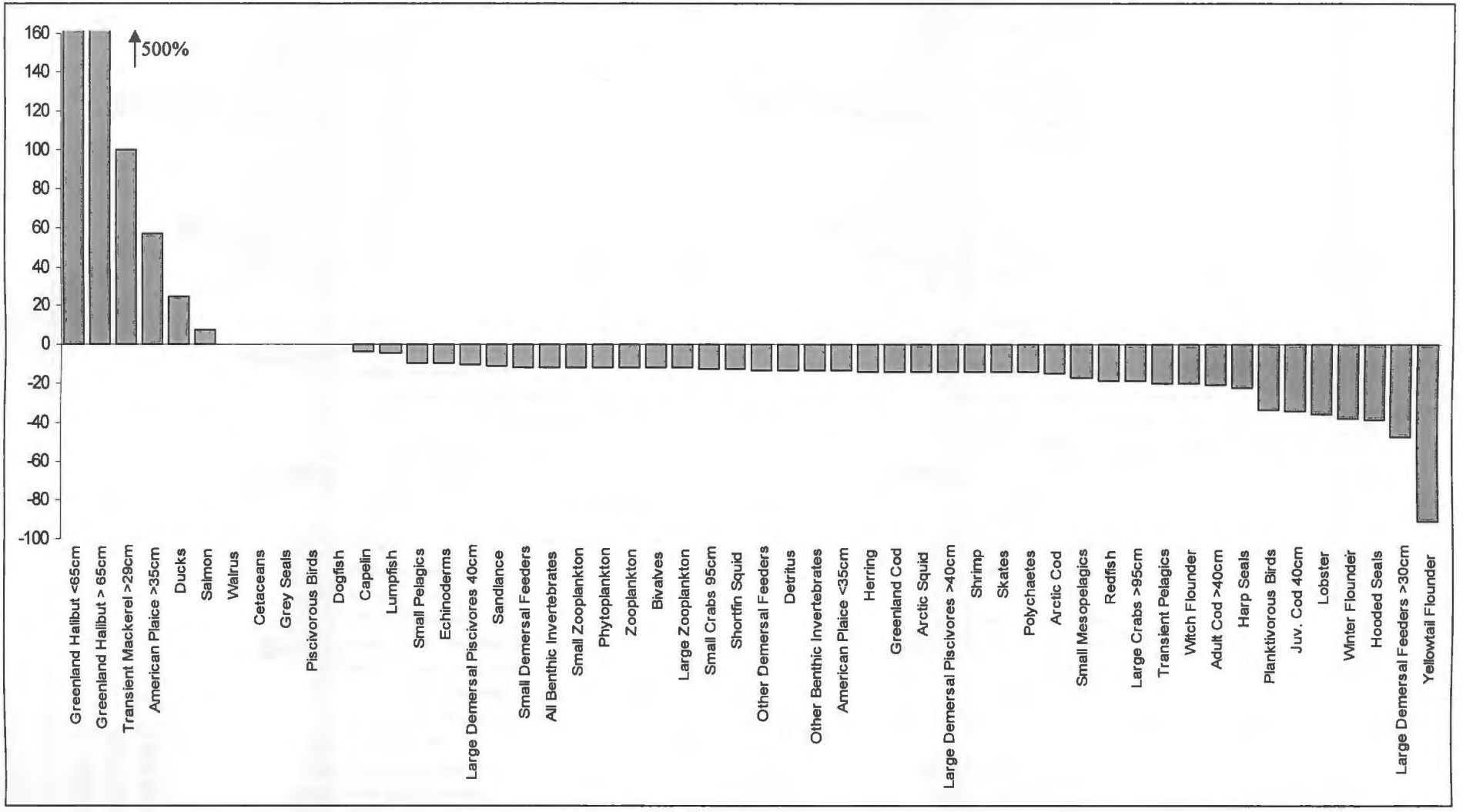


Figure 4.3: Percent Change in Biomass of species groups from 1954 to 1970 (Note the percent increase in biomass for Greenland halibut >65cm and <65cm both exceed 500%).

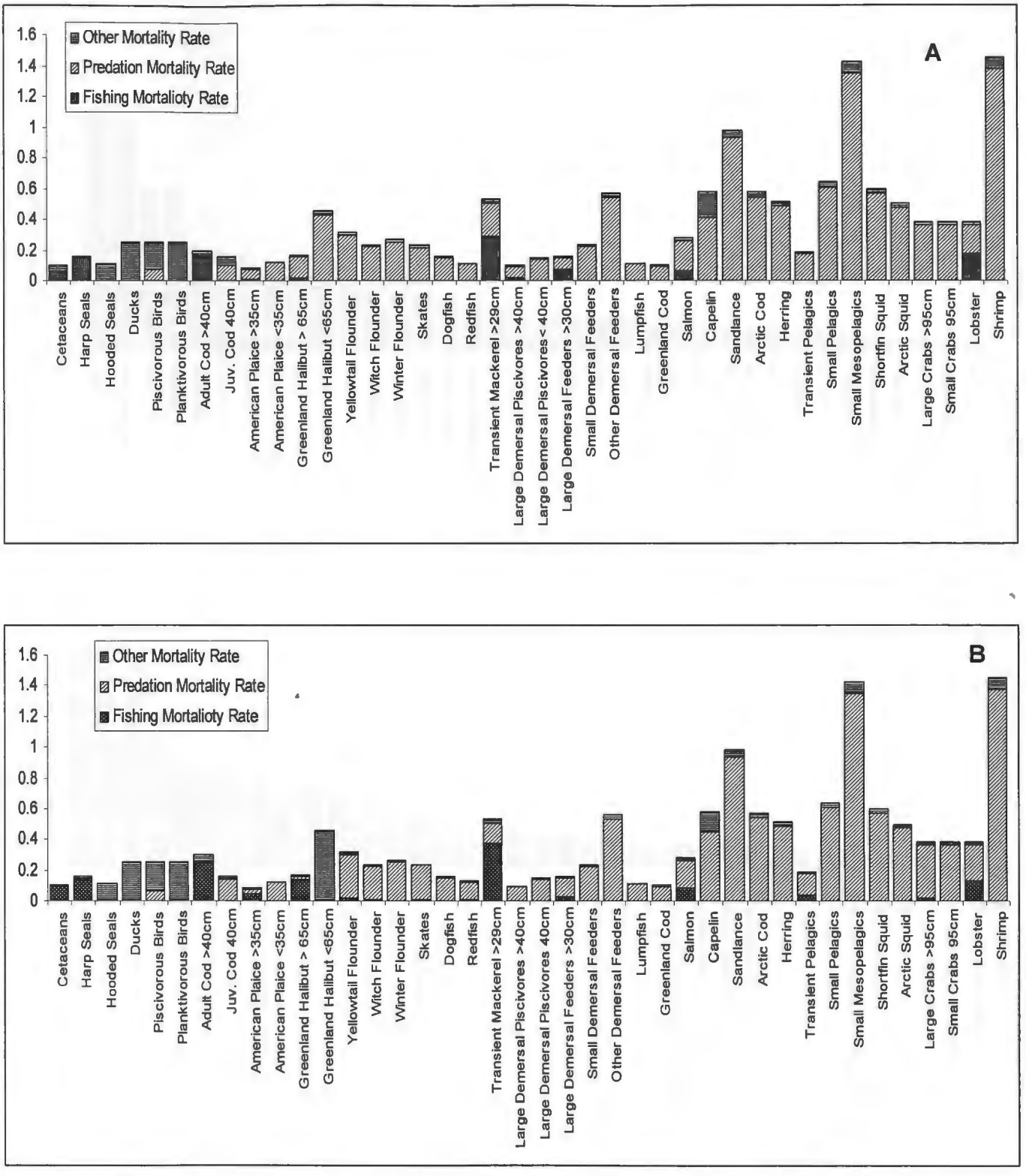


Figure 4.4: Total Mortality of species groups divided into fishing mortality, predation mortality and other mortality for the mid-1950s model (A) and the late 1960s model (B).

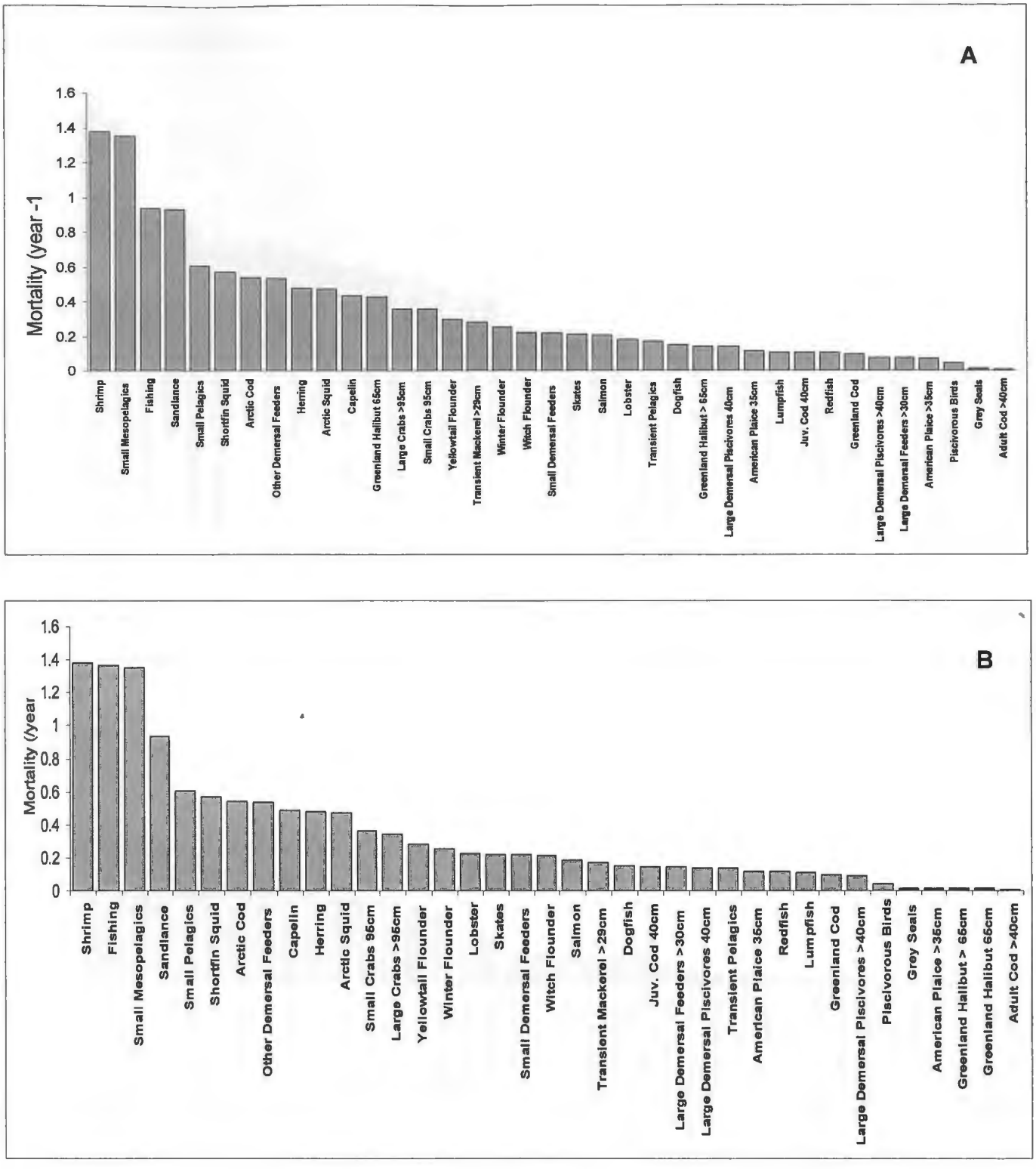
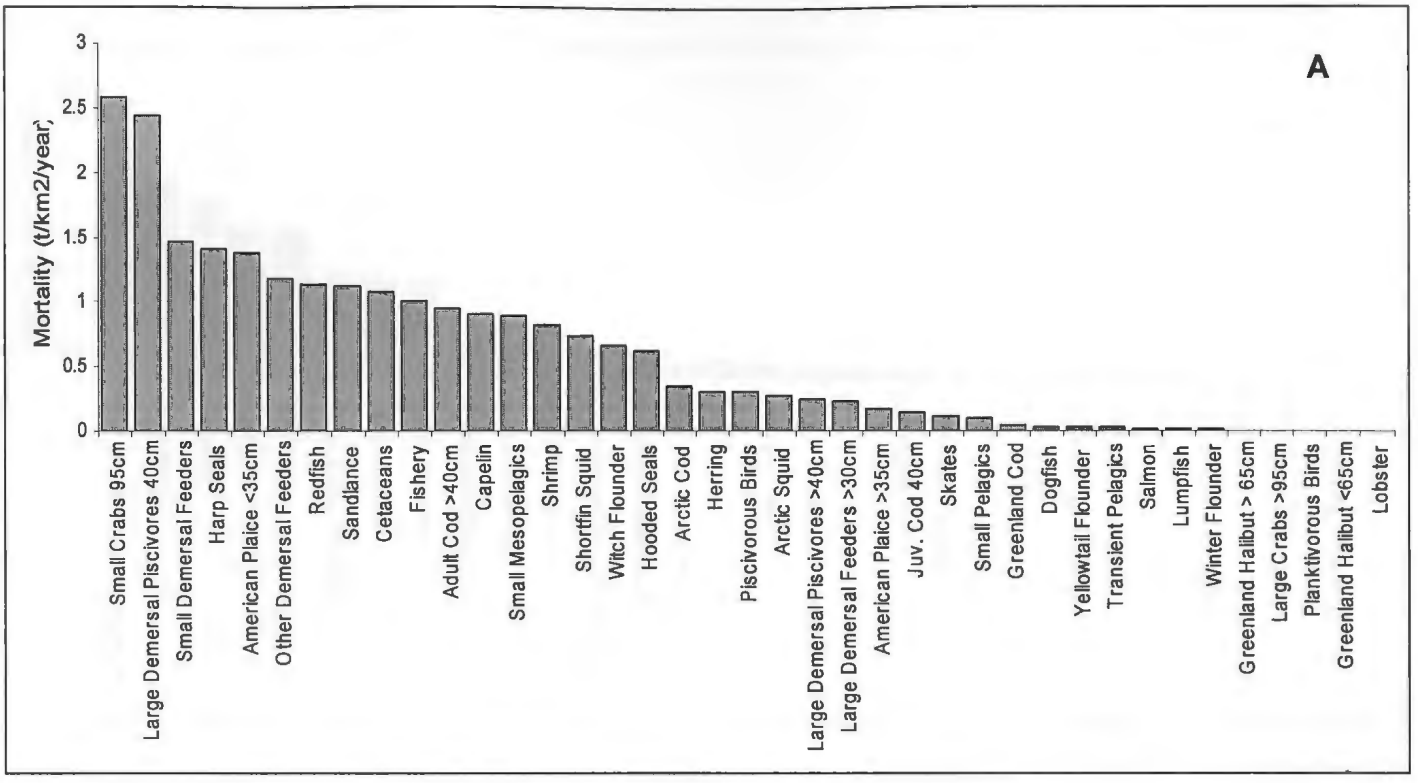


Figure 4.5: Distribution of Predation Mortality among all prey groups in the mid-1950s model (A) and in the late 1960s model (B)(includes the fishery as a predator).



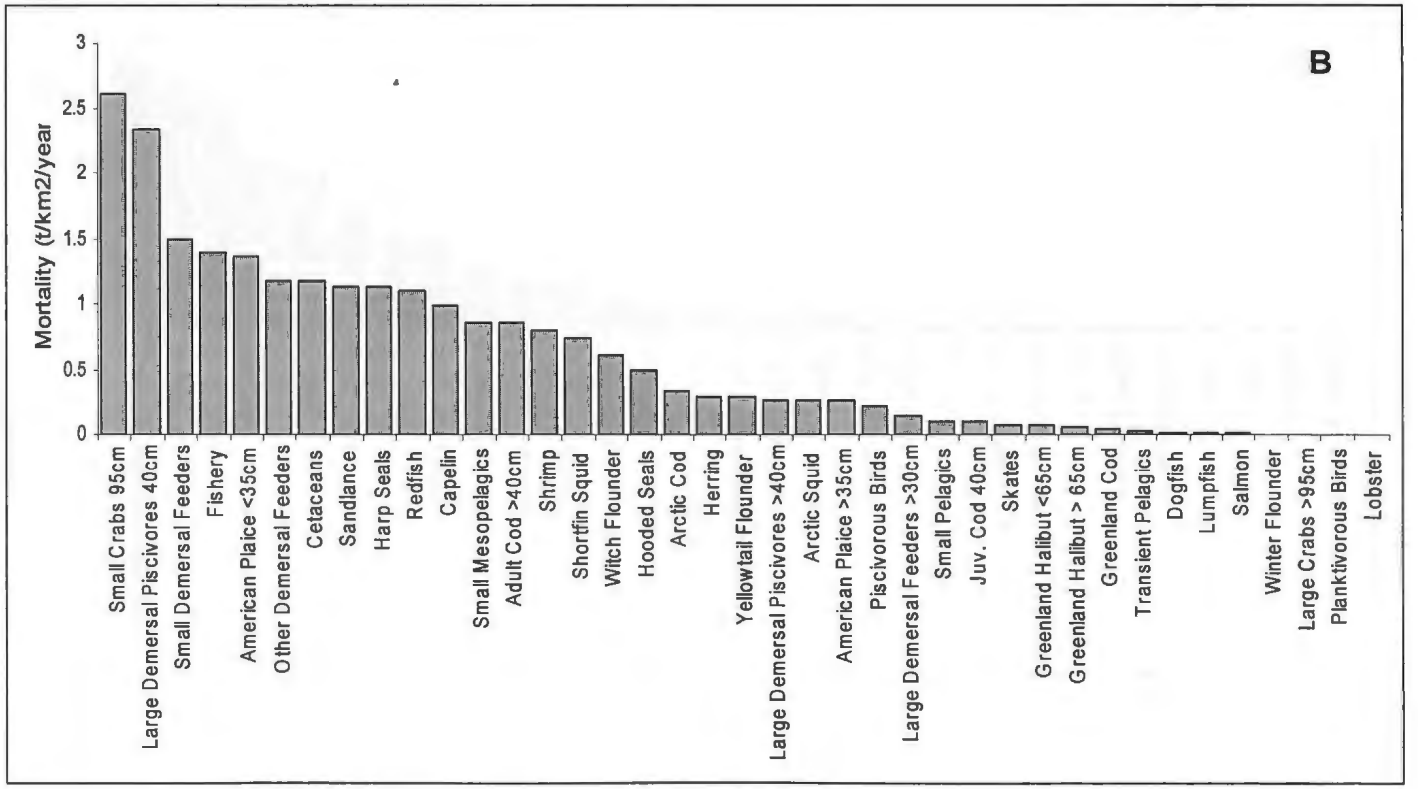


Figure 4.6: Distribution of predation among all predators, includes the fishery (A= mid-1950s model, B= late 1960s model).

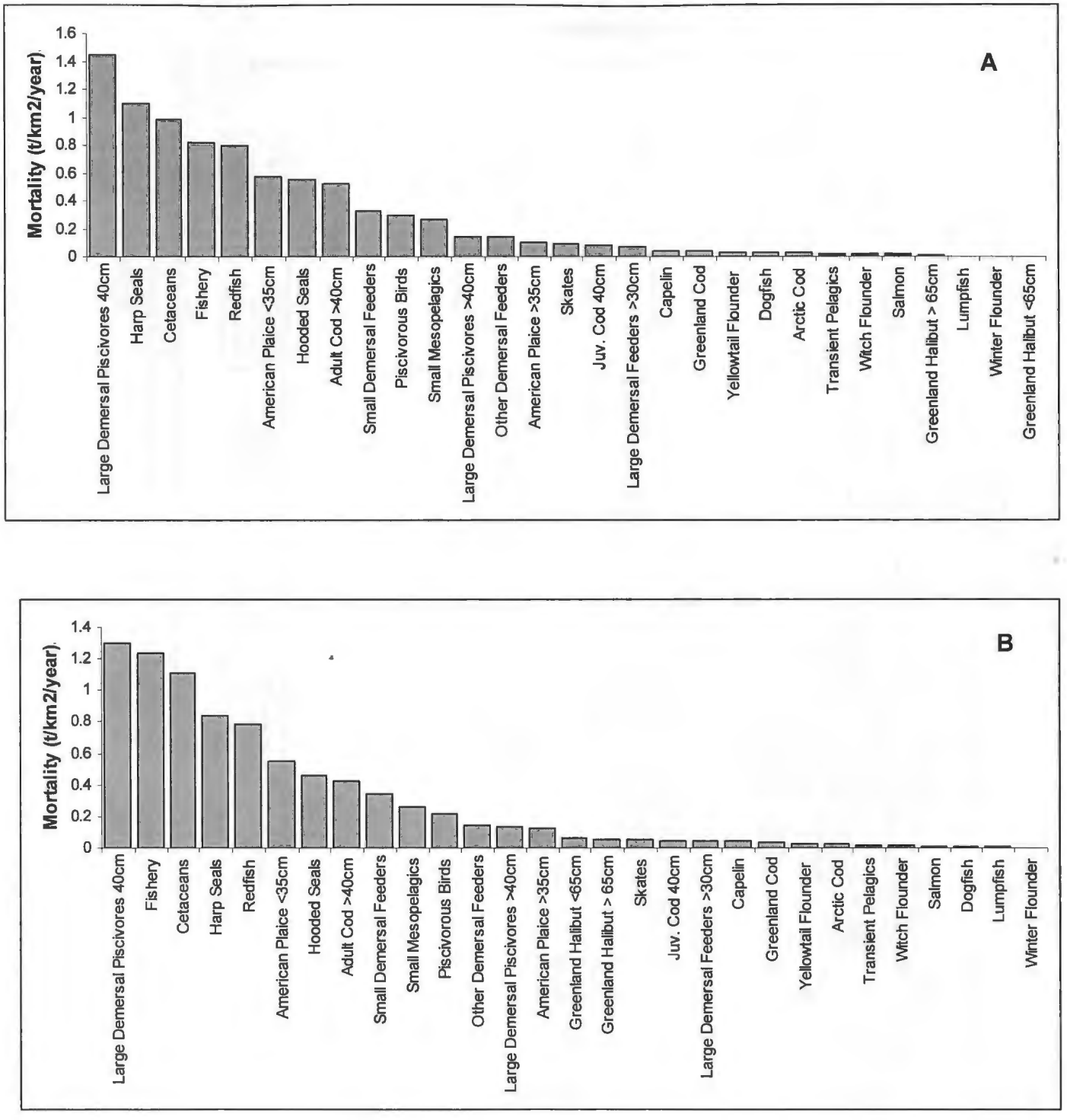


Figure 4.7: Distribution of predation mortality among vertebrate prey, includes fishing (A= Mid-1950s model, B= Late 1960s model).

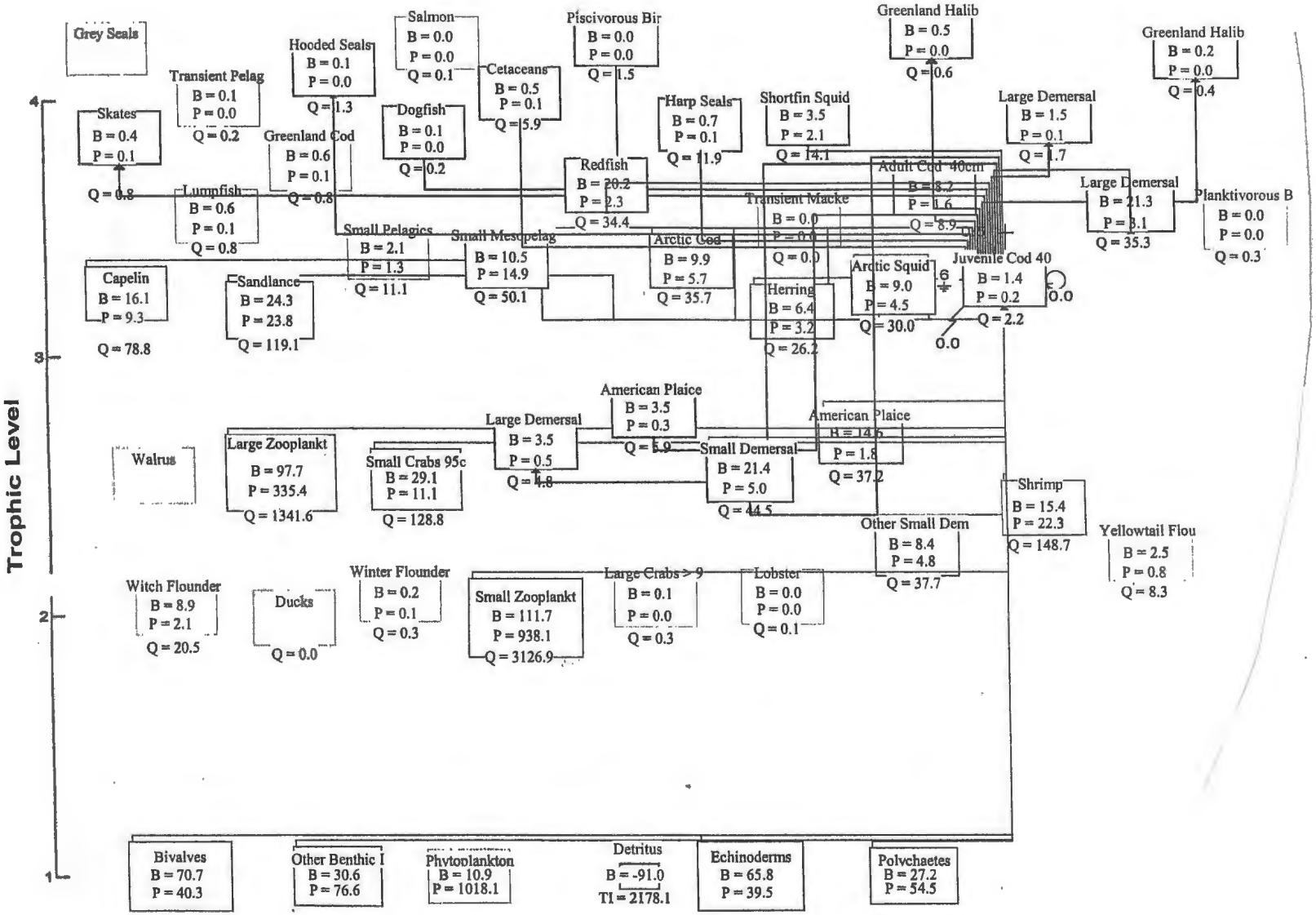


Figure 4.8: Ecopath Flow Diagram illustrating the role of Juvenile cod <40cm. Arrows leading away from top of box indicate predators of this species group, while arrows coming from the bottom of the box indicate the prey of Juvenile cod <40cm.

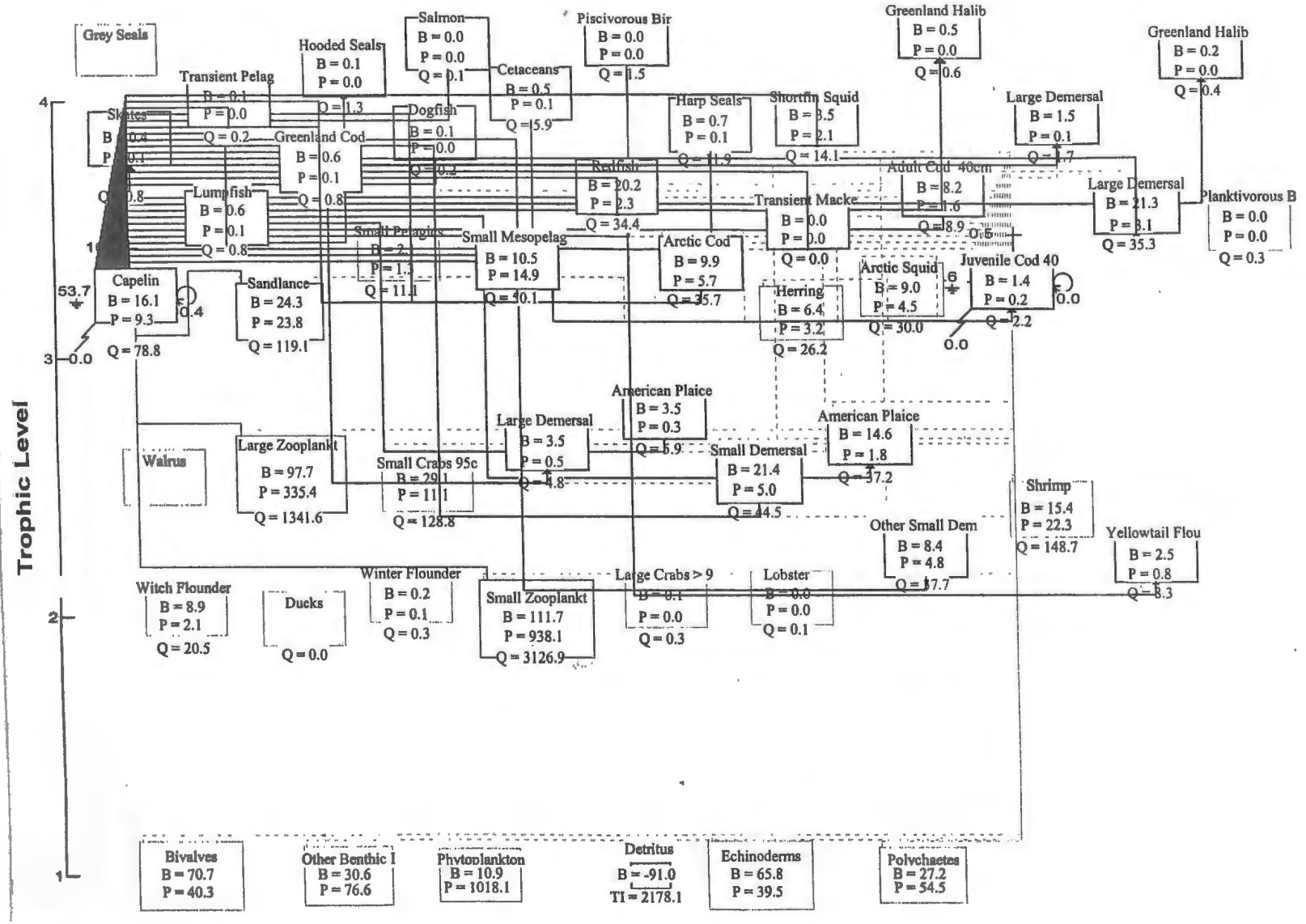
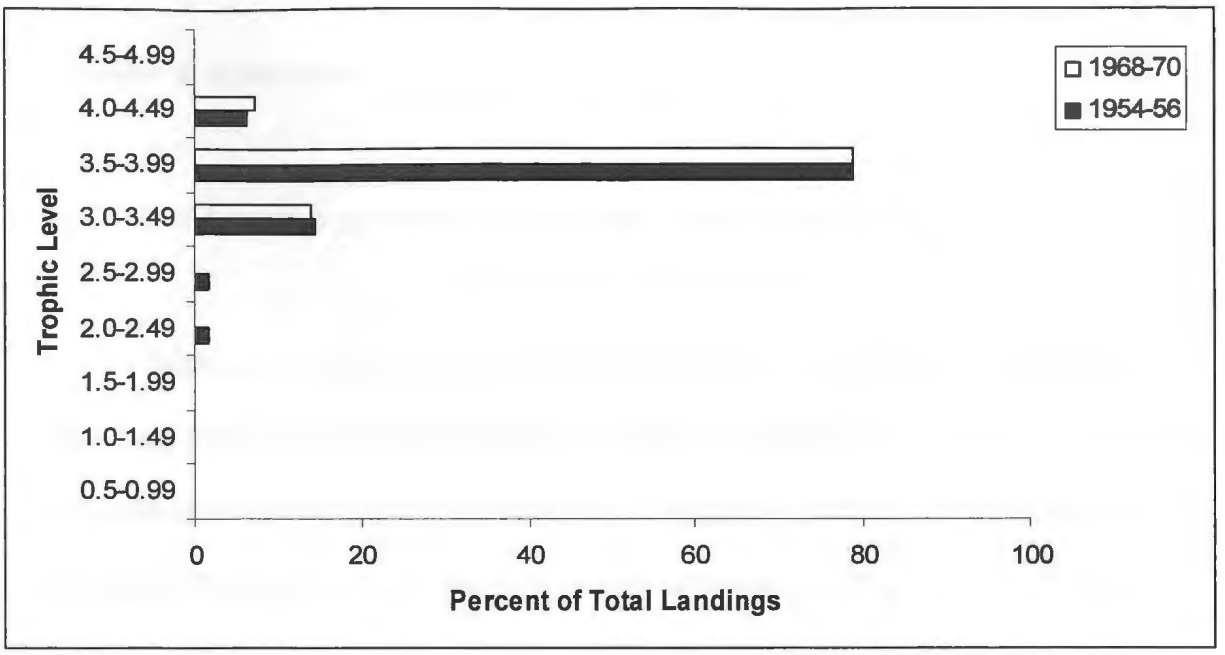


Figure 4.9: Ecopath Flow Diagram idicating the role of capelin. Note many predators of this species group with arrows leading towards this box. Dotted lines in background indicate role of Juvenile cod from previous figure.

A



B

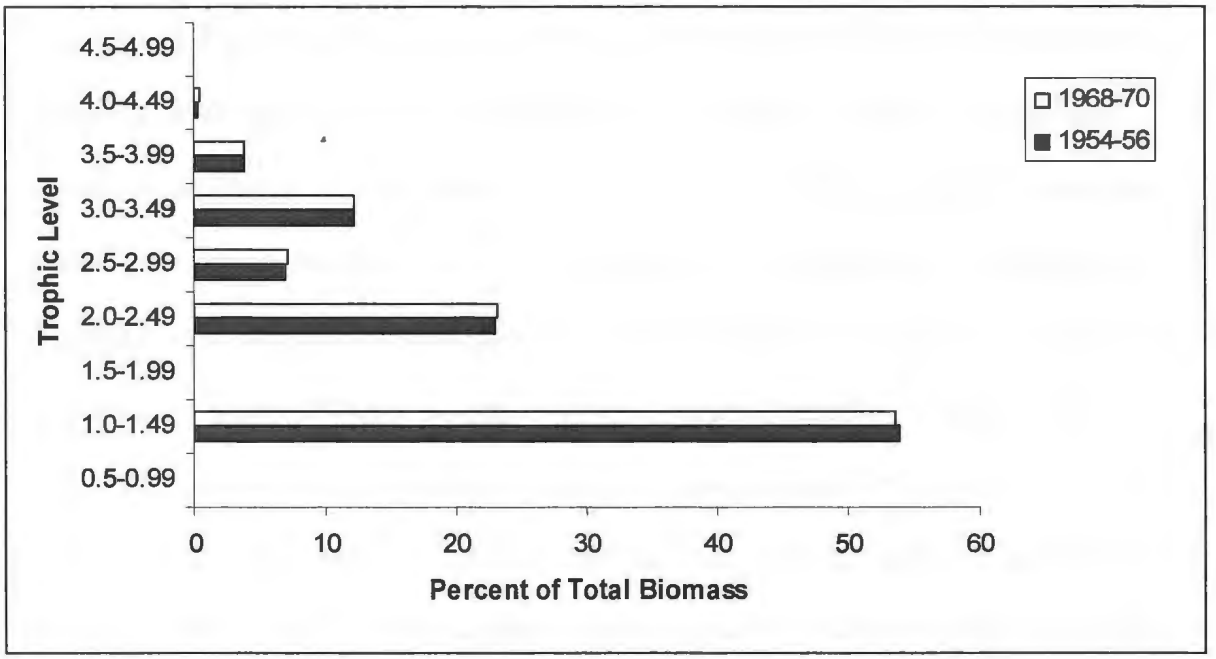


Figure 4.10: Percent of Landings (A) and Biomass(B) by Trophic Level, comparing the mid-1950s model and the late 1960s model.

Chapter 5: Discussion

5.1 What did I expect the difference to be between the two systems?

Pauly *et al.* (1995) among others, describe a global 'fishing down' phenomenon occurring over the past fifty years. The shelf off Newfoundland and Labrador is one of the systems included in this world wide trend (Pauly *et al.*, 1998). There are descriptions throughout the history of Newfoundland and Labrador and Canada about the wealth of sea life in this area. Countless recent publications on the current state of our oceans provide bad news on the state of global fisheries, *e.g.*, Myers and Worm (2003), Hilborn *et al.* (2003) and Pauly and Maclean (2003). Part of the challenge in considering how the ecosystem of the past turned into the ecosystem of the present is approximating when significant ecological events occurred. We know where the human populations were and what they removed from the system, which includes the technological innovations that allowed for more efficient resource harvesting, i.e., we have a sociological, economic and technological history. What is lacking is a finer ecological time line of how and when marine populations have responded to human and environmental influences.

Taking into account the fishing activity on the Newfoundland and Labrador Shelf between 1954 and 1970, as summarised in Chapter 2, and the nature of the ecosystem in this area in current times, one might expect major changes to have occurred by 1970. Looking back at the whole Newfoundland and Labrador shelf and considering the heavy

fish harvesting leading up to the 'killer spike,' what changes in the ecosystem would be expected to occur?

In view of the increasing landings of many fish species throughout the time period between 1954 and 1970, an overall decline in the biomass of those species in particular would be expected and perhaps some corresponding growth in some of their main prey species. Groundfish species would be expected to decline a great deal in the face of such a fishery while invertebrates such as snow crab, which have come to fill the ecological and economic niche left by the groundfish collapse, might have started to increase.

I also expected that for several species groups, there would not be much difference between the early 1950s and the late 1960s. The marine mammal populations had already experienced significant decline in population numbers before the mid-twentieth century and not much change was expected. Harp seals, for example had been hunted for centuries in the area; by 1844 between 100000 and 500000 were being exported annually (Sanger, 1998). Hence, major declines due to hunting pressure took place long before the 1950s. Similarly whaling had occurred in the northwest Atlantic for centuries, starting in the sixteenth century with the Basques (Sanger, 1998). The Great Auk is one of the most famous of the now extinct animals from the Newfoundland and Labrador shelf region. It and many other seabird species were used by Europeans and First Nations as food, bait and sources of oil and feathers, i.e., coastal seabird populations had long been impacted by humans before the arrival of any large scale fisheries (Montevecchi and Tuck, 1987).

Predator/prey relationships may be expected to change when a large fishery is imposed on an ecosystem. Ecosystem relationships might shift in response to changes in prey abundance, new availability of prey species and changing competition (Lilly, 1987). Lilly (1987) provides an example of this; he suggests that the survival of juvenile cod might improve in years with increased capelin abundance as adult cod could feed more on the capelin; conversely there could be a negative effect on the juvenile cod as they compete with capelin for food. Predator/prey interactions are complicated and will likely remain very similar between the models due to limitations in the data.

When considering the trophic organisation of the two ecosystems, given the intensive fishing effort directed primarily at groundfish throughout the 1950s and 1960s, the mid-1960s model should be closer to what we would expect from a system that has been 'fished down' when compared with the mid-1950s model. If the offshore ecosystem in the early-1950s is assumed to be largely untouched, except for the species described above, it might be ascertained that it is still well developed, as the species had been established for hundreds or thousands of years. The concentrated harvests between this time and the late-1960s might have spurred some new development among species further down in the food web. Increased production among species lower in the food web would point to the mean trophic level of the system in the late-1960s model being slightly less than that of the mid-1950s model. As fishing fleets diversified and used new technologies, such as midwater trawls to target pelagic species (often prey for species caught in bottom trawls), the mean trophic level of the catch taken from the ecosystem is sure to have been less by the late 1970s.

Many of the shifts that have occurred in the making of the current ecosystem of the Newfoundland and Labrador shelf have occurred since the killer spike in 1968. While this was the year of the peak fishery with at least 800000 metric tonnes of Atlantic cod captured (Hutchings and Myers, 1995), cod fisheries continued to expand and intensify into the 1970s and 1980s even after the extension of the 200 mile Exclusive Economic Zone.

5.2 The Model Results- What is the difference between the two time periods and why?

As described in Chapter 2, the Newfoundland and Labrador shelf sustained a massive fishery between 1954 and 1970. The models representing the ecosystem for these two time periods, however, are remarkably similar. According to the models, there are some biomass declines, but not at the magnitude suggested by comparing models between 1900 and the mid-1980s. The roles of predators and prey are very much the same because the same diet information was used in both models and the system statistics indicate that the modelled ecosystems are not dissimilar when it comes to the trophic organization and extent of fishing down (Table 4.5).

5.2.1 Biomass

The estimates of biomass for most species groups in the mid-1950s and late 1960s models fit well the trend previously implied by the models constructed for 1450, 1900,

1985-87 and 1995-97. For several of the species groups (cetaceans, harp seals, hooded seals, ducks, piscivorous birds, planktivorous birds, adult and juvenile Atlantic cod, adult and juvenile Greenland halibut, skates and capelin) biomass was estimated from a combination of historical sources, taking into account the trend suggested by Heymans and Pitcher (2002). The remaining species groups were estimated by Ecopath. In most cases, the biomass estimated by the Ecopath models for the mid-1950s and late-1960s were points along the trend created from other model estimates.

There are a few of groups that showed a different trend (See Chapter 4). American plaice > 35 cm, did not follow the trend as the biomass estimated for 1968-70 is quite an increase from that in the 1954-56 (See Figure 4.1:F and Figure 4.1). This is surprising because the biomass estimated in the mid-1980s model, calculated from Engels survey trawls (Heymans and Pitcher, 2002), is quite low (Appendix 2). Part of the reason for the apparent increase in biomass throughout the first half of the century, may be related to the estimate of fishing mortality. There is no reported commercial catch of American plaice before 1950 (Morgan *et al*, 2000), though Heymans and Pitcher (2002) did assume a small landings value for American plaice as part of a First Nations catch in 1900. In the mid-1950s model, there was more American plaice landed, which can tend to increase the biomass estimate slightly, i.e., the historical estimate was too low. In the late-1960s model, the biomass estimate is high and the landings are larger than in the mid-1950s model. While it is possible that the species experienced a period of population growth, Koslow *et al.*,(1987) predict a 7-10 year periodicity in many groundfish species in parts of the Newfoundland and Labrador Shelf, the apparent increase in biomass in the

model version of the ecosystem likely had more to do with American plaice's role as a predator. The largest part (70%) of its diet is made up of invertebrate groups (40% echinoderms, 8% bivalves and 10% other benthic invertebrates (Heymans and Pitcher, 2002)), all of which have very high biomasses which could certainly accommodate the growth of this predator. Harp seals, the main predator of American plaice >35cm are a less significant predator in the late 1960s model (Figure 4.6) due to a decrease in biomass, likely reducing predation pressure on adult American plaice (Appendix 1).

Biomass estimates for large demersal feeders > 30cm were slightly higher than expected, particularly for the mid-1950s model. This group contains groundfish species such as haddock, longfin and red hake, wolffish, and the grenadiers. In the time period between the 1900 model (Heymans and Pitcher, 2002) and the mid-1950s model, this group experienced the largest percent increase in biomass, and between the mid-1950s and late-1960s models, it had the second largest percent decrease in biomass (See Figures 4.2 and 4.3). This is quite unlike the trend in biomass for most other groundfish species. Some of the species within this group had very heavy landings as reported in the ICNAF statistical bulletins in the very early 1950s. Haddock was a very important target species in the earliest trawler fisheries and was targeted in particular by countries like Spain (ICNAF, 1956). The historical biomasses approximated for large demersal feeders >30cm may have been underestimates considering the landings sustained through the 1950s; the authors of the 1900 model suggest that some of the input parameters for this species group should be adjusted (Heymans and Pitcher, 2002). Haddock populations, in particular, were thought to have crashed quite early in the era of industrial fishing

(Vasconsellos *et al.*, 2002), and this may account for the large decrease in biomass between 1954 and 1970 (Figure 4.3). A crash in the population on haddock on the Newfoundland and Labrador shelf early in the time of the factory freezer trawler fishery is consistent with historical records.

Another species group that departs from the apparent biomass trend in models completed by Heymans and Pitcher (2002) is large crabs >95cm, which includes snow crab, jonah crab, red crab and Northern stone crab. The biomass calculated for the mid-1950s is relatively low when compared with the biomass estimates for 1900 and the mid-1980s (See Figure 4.1:AH). This result was puzzling and all of the input parameters surrounding this species group were re-examined to determine if there was a mistake. In the original running of the historical models, 95% ecotrophic efficiency was assumed in order to calculate a biomass for the group, as there is very little information on the historical abundance of some of these species. Heymans and Pitcher (2002) had trouble balancing the large crab > 95cm group as they were not consumed according to their model parameters and so, in an effort to balance, they employ a biomass estimate equal to that used in their model of the mid-1980s, adapted from Bundy *et al.* (2000) which had been determined from a scientific study (Dawe *et al.*, 2000). These values can be considered reliable for the mid-1980s but they produce a problem when considering the long-term biomass trend for the species group. Considering what we know about the current ecological role of the snow crab on the Newfoundland and Labrador Shelf, an increase in biomass throughout the 1970s would not be surprising. The apparent decline throughout the first fifty years of the century is a consequence of allowing Ecopath to

calculate the biomass in the mid-1950s and late-1960s models, in the absence of information on this species group. I am aware of a large amount of discarding of crab out of gill nets used to fish cod; this along with reports of damage to crab habitat by trawling could explain a shift in the biomass of crab (Bundy, 2001).

5.2.2 Predator Prey Relationships and Mortalities

In Ecopath ecosystem models the production/biomass term for every species group is assumed equal to the total mortality for that group. As explained in Chapter 4, for the majority of species groups in the mid-1950s and late-1960s models the P/B term entered was the same as that used by Heymans and Pitcher (2002). Heymans and Pitcher (2002) calculated the total mortality (z), using Pauly's equation, assuming total mortality was close to natural mortality (See Section 3.2.2). As can be viewed in Figure 4.4, the total mortality does not change for most species between the two time periods, but in several cases the proportion of that mortality attributable to fishing, predation or natural causes, does change. Fishing and predation mortality covers most of the mortality among species groups in both models. In marine ecosystems, the majority of the production is used for the fishery and predation, while very few individuals die of old age or diseases (Christensen and Pauly, 1998).

There is a notable increase in the relative fishing mortality for the species groups cetaceans, American plaice >35cm, Greenland halibut >65cm, yellowtail flounder, and transient mackerel >29cm during the late 1960s. There are minor increases for several

other species (See Figure 4.4 and Tables 4.3 & 4.4). This is hardly surprising, considering the increase in landings for many species throughout the time period between the two models. According to NAFO, American plaice landings grew extensively leading up to the late 1960s; before the early 1960s American plaice landings hardly reached 20000 metric tonnes, but in 1967, they were close to 100000 metric tonnes (NAFO, 2004). Similarly, yellowtail flounder landings were never reported above 100 metric tonnes before the early 1960s but reached 40000 metric tonnes by 1970 (NAFO, 2004).

Changes in predation mortality were also observed. Adult Atlantic cod were preyed upon at the same level in both models while juvenile Atlantic cod are more heavily preyed upon in the model representing the late 1960s. Most groundfish species are the opposite, with higher rates of predation in the earlier time period. This would be expected because as top predators are removed from a system there would be less predation on species in mid-trophic positions. Shrimp are the most heavily preyed upon species group in the models representing 1954-56 and 1968-70. Small mesopelagics (lanternfishes, pearlsides and barracudinas) and sandlance are the second and third most preyed upon. The fishery places differently in the two time periods. In the mid-1950s model, the fishery take is in the third position, i.e., more fish are taken from the system than are consumed by predators for all but two groups. In the late-1960s model, the fishery take is exceeded only by the predation mortality on shrimp. Note that this is the fishery take on all species compared with predation mortality on individual species, added for comparison purposes only.

Only a few groups changed considerably between the mid-1950s and late-1960s modelled systems with respect to the amount consumed by predators. Greenland halibut < 65cm are preyed upon far less in 1968-70 than in 1954-56. In the mid-1950s model, juvenile Greenland halibut make up 5.5% of the diet of harp seals, 6.3% of the diet of Atlantic cod > 40cm and 18% of the predation by large demersal piscivores > 40cm. In the late-1960s model, they are no greater than 3% of the diet of any species. Similar results were found for Greenland halibut > 65cm, transient mackerel <29cm and large demersal feeders > 30cm. Juvenile Atlantic cod are the only species group that were preyed upon more heavily in the late-1960s model. The biomass of several predator groups increased in the system and their predation level also increased. The increase of predation mortality on Atlantic cod <40cm is due to increased consumption by a number of predators on a decreased biomass. According to the models, juvenile cod are a part of the diet of many species groups, but never much more than 2-3% of the total predation of any individual predator group. The predation mortality inflicted on juvenile cod in the late-1960s model, is sometimes only 0.1% greater than it was in the mid-1950s model for any one predator group and hence sums to a greater predation rate overall.

In both models small crabs <95cm are the number one predator in terms of the amount of predation mortality that they inflict per year. Small crabs <95cm consume other smaller invertebrates, their diet consisting of 35% zooplankton and 25% bivalves (Heymans and Pitcher, 2002; Lovrich and Sainte-Marie, 1997). Large demersal piscivores < 40cm and small demersal feeders are the second and third most important predators for both time periods. The large demersal piscivore (<40 cm) species group is

made up of white hake, silver hake, monkfish, sea raven, cusk and Atlantic halibut. The size of this species group suggests they are primarily juveniles. This group has a varied diet, consisting mostly of large zooplankton (24%) and shrimp (12%); other prey groups range from 9% capelin to 7% on their own species group (See Appendix 1). Small demersal feeders include the smaller and often juvenile members of the group that includes haddock, longfin hake, red hake, wolffish, grenadiers, eelpouts and batfishes. This group has a diet focussed on few species groups, with more than 90% of their diet consisting of the invertebrate species groups. It is interesting that when all predators are taken into consideration, predators that focus on fish groups match the quantities of prey consumed by invertebrate predators. In fact, in the mid-1950s model, among the top seven predators, that make up 50% of the total predation in the system, only one species group, harp seals, is primarily a predator of vertebrates. The same is true in the late-1960s model, though in this case the only predator focussing primarily on vertebrates is the cetacean group.

The fishery can also be thought of as a predator. In 1954-56, the outset of major industrialised fishing on the Newfoundland and Labrador Shelf, the amount of fish taken in the fishery ranked tenth, behind the amount of predation mortality attributable to nine other top predators (See Figure 4.6). In 1968-70, the fishery became the fourth most important predator on the Newfoundland and Labrador shelf.

The fishery, as a predator, is perhaps better represented in Figure 4.7, where it is considered against predators on vertebrate species only. This is reasonable, since the early industrial fishery would not really be competing as a predator for prey with species

groups like the small demersal feeders (which consume mainly invertebrates). Contemporary fisheries, harvesting several invertebrate species like shrimp and crab, would be a competitor across the whole system. Large demersal piscivores >40cm are the dominant predator on vertebrate prey in the mid-1950s and the late-1960s. This group, made up of the larger adult white and silver hake, cusk and Atlantic halibut, eat more than 40% of other demersal groups and about 30% capelin and sandlance. Harp seals, as predators, place second in the mid-1950s model and fourth in the late 1960s model, while cetaceans, place third in both models. Whales and porpoises eat Arctic cod, capelin and small pelagics like juvenile mackerel and Atlantic rainbow smelt. The fishery comes in second place as a significant predator in the late-1960s model and fourth place in the mid-1950s model. That is, the fishery in 1954-56 took more fish than all but three predator groups and all but one group in 1968-70. It is interesting to note that in the late 1960s large demersal piscivores <40cm consumed more fish than were taken in Hutchings and Myers (1995) 'killer spike.' It is clear that the fishery was as important an influence on the species contained within 2J3KLNO as many of the apex predators in both time periods. Indices that compare the fishery take with predation rates would be a useful tool today, when some predator species like harp seals are often credited for the continuing low numbers of species like Atlantic cod. Population dynamics can be complicated when man is a predator (Fowler, 1995).

5.2.3 Odum's Ideas

In 1969, E.P. Odum published an article in *Science* that put together a collection of hypotheses integrating trophic dynamics and community structure in order to predict and describe how communities tend to develop over time. The theories and system of ratios of Odum have been much debated since their original publication and are questioned as descriptions of aquatic ecosystems. Odum's systems of reference were terrestrial, forest ecosystems, where there are quite different dynamics, including competition for space, resulting in plant succession. More recently, Link (2002) has suggested that there is a need to modify the way we look at marine food webs as they are inherently very different from terrestrial and freshwater systems. Christensen (1993), however, developed a method by means of which Odum's twenty-four ecosystem attributes can be quantified and Ecopath has incorporated these ratios, using them to examine the system characteristics and the size of the system in terms of flow and trophic dynamics, upon the completion of an ecosystem model.

System statistics can be organised into three main groups (See section 4.1.3 and Table 4.5). The first group of parameters describes the systems in terms of the amount of flow. The second group of parameters describes the fishery in the system and where it is focussed, i.e., the mean trophic level of the catch and the overall efficiency of the fishery. Finally the third group of parameters characterises the ecosystem in terms of ratios.

The late-1960s model is clearly different from the mid-1950s model in terms of the first group of system statistics (See Table 4.5). The sum of the total consumption,

exports, respiratory flows and flow to detritus is equal to the total system throughput (Ulanowicz, 1986). The ecosystem represented by the mid-1950s model is larger than that of the late-1960s model in terms of each of these elements representing the amount of flow. It also has a greater amount of total production and a larger biomass (excluding detritus).

The second set of parameters relating to the catch shows the mean trophic level of the catches in both models to be the same. As the fishery fleet expanded their spatial range and gear capabilities (Chapter 2), they harvested more elements of stock complexes in traditional species and began harvesting a lot more pelagic species. In 1954-56, however, there were more fish harvested at the lower half of trophic level three (Figure 4.10). Pauly *et al.* (1998), report that the global marine mean trophic level of landings declined from above 3.3 in the 1950s to less than 3.1 in the mid-1990s; the trophic level of the catch in 2J3KLNO is considerably higher at 3.87. Pauly *et al.* (1998) also suggest that global fisheries are decreasing about 0.1 trophic level per decade. Pauly *et al.* (2001), note that the mean trophic level of fish landed on the east and west coasts of Canada declined between 0.03 and 0.1 trophic level per decade.

The mean TL (trophic level) of fish landed can be used as an index of sustainability in multispecies fisheries. Its reliability will depend on the quality of the data and the length of the time series available for analysis (Pauly *et al.*, 2001). Mean TL can combine a vast array of biological features pertaining to the species within the ecosystem. A decline in TL and a decline in catches can help to solidify evidence of a

lack of sustainability at the ecosystem level (Pauly *et al.*, 2001). In this case it would be difficult to say much about the sustainability of the two modelled systems.

Gross efficiency is the sum of fishery catches relative to the total amount of primary production. This value will be higher in systems where the fishery is focussing more upon species low in the food web (Christensen and Walters, 2000). The late 1960s model, has a far higher gross efficiency than the mid-1950s model (See Table 4.5), which is nearer the global weighted average of 0.0002 (Christensen and Walters, 2000). This may indicate that the fishery in 1954-56, was relatively undiversified or, that it was more focussed on apex predators compared with the late 1960s. Considering the history of the offshore fishery, both may have occurred, as the fishery did little to diversify up to that point and was more focussed on Atlantic cod, redfish and flounder species.

Trites *et al.* (1999), using a direct reference to Odum, suggest that fishing tends to reduce the 'maturity' of an ecosystem; similar links are found in Christensen (1995). The third group of system ratios relates to the stage of development or the extent of fishing down in the systems represented by the mid-1950s and late-1960s models and they are not as easy to interpret as the first two sets of system ratios. The model representing the Newfoundland and Labrador Shelf in the late-1960s is slightly greater than that of the mid-1950s in terms of the ratio of total primary production over total respiration and total primary production over total biomass. In the early developmental stages of a system, the production is expected to be higher than respiration, leading to a ratio greater than one (Christensen and Walters, 2000) and this is the case in both models. The value in the late 1960s model is slightly higher suggesting that the system at this time period is in an

earlier stage of development. The ratio of primary production over the biomass indicates the opposite. In the early stages of ecosystem development, production exceeds respiration and hence biomass accumulates (Christensen and Walters, 2000), and so in this case the model with the lower value (the mid-1950s model here) is considered to be at an earlier developmental stage. Finally there is the net system production, which is the difference between total primary production and total respiration and should be large in systems which have not been subjected to fishing down. The net system production is a little larger in the mid-1950s model and suggests that this system was in a slightly earlier developmental stage compared with the late-1960s model. With the differences in the 'maturity ratios' being so slight, it is difficult to say, using these ratios, whether one of the ecosystem models represents one system that has been more fished down than another. The lack of differences among these three ratios may well be due to the unsuitability of such ratios to aquatic ecosystems; these system ratios are dominated by species groups at the lowest trophic levels which would have little if any response, if at all, to 'disturbances' by fisheries. In addition, the uncertainty attached to many of the input parameters included in these models leads to artificial representations in the system ratios (Gomes, 1993).

There are a few other parameters offered with the system statistics, also relating to development. The mid-1950s and late-1960s models are equal in the ratio of total biomass over the total system throughput. They are also equal in a term called the Connectance Index, the ratio of the number of trophic links between species groups to the total possible number of links (Christensen and Walters, 2000). Finally, the last

parameter is called the System Omnivory Index, which is a measure of the distribution of the feeding interactions among the trophic levels (Trites *et al*, 1999). The mid-1950s and late-1960s models have the same Omnivory Index. In using identical diet information for the mid-1950s and late-1960s models, these ratios would not be expected to change. These system statistics would be more useful in comparing systems from different geographical areas.

5.3 Why is the difference between the two models not what was expected?

The model results do show an overall decline in biomass among many important species, as well as, a marked increase in fishing mortality. The fishery also proved to be a serious competitor with the natural predators in the ecosystem on the Newfoundland and Labrador shelf. The analysis of trends in trophic level of the systems represented in the models suggest a moderate a decline in the trophic level of the ecosystem and no decline in the trophic level of the fisheries catches as suggested by Pauly *et al.* (1998), particularly when compared with the levels experienced in the 1980s and 1990s models (Heymans and Pitcher, 2002); this suggests that there was a more dramatic trophic shift during the 1970s.

In the case of Atlantic Cod, one might have expected a larger decline in abundance between 1954 and 1970, especially considering the landings in the area during that time. However, the modelling results show that a larger part of the decline actually

occurred throughout the 1970s, culminating in eventual stock collapse. This appears to be true for many species; the more intense declines in species biomass occurred throughout the 1970s so that generally there is not as much difference between the two models discussed here as had originally been expected.

In Chapter 2, the Hutchings and Myers (1995) 'killer spike' in 1968 is identified as the time period when fishing vessels took more fish from the Newfoundland and Labrador Shelf than in any one previous year. The landings that year also exceed the annual landings throughout the 1970s. There are two possible explanations for why the ecosystem does not appear to have responded substantially and immediately to this intense fishing pressure: the make-up of the biological populations, or what the model design will allow us to see, given the available data. Pimm *et al.* (1991) mention that the weakness in available data is one of the main shortcomings of all food web research.

When one considers the nature of age-structured biological populations, a 'lag' in the decline of the cod and other groundfish stocks in response to heavy fishing pressure may be expected. There are two important factors about the populations to consider: the longevity of the species targeted and their behaviour. Long-lived species normally supply a large yield when a fishery is new as it takes a while to fish down all of the older age classes (Hilborn and Walters, 1992). On the Newfoundland and Labrador shelf, if we are assuming that the offshore component of the ecosystem had been mostly unaffected by fisheries before the arrival of factory freezer trawlers, a large component of the marine populations would have been comprised of older age classes or cohorts. If there were several cohorts available, it would likely take at least as many years (as there are cohorts)

for real declines to be observed in the stocks, i.e., there would have been sufficient older age classes to reproduce and 'make up for' the losses to fisheries until all of the older age classes are captured (Jennings *et al.*, 1999). Fisheries stock assessment often considers the idea of surplus production, which is the amount of catch that can be taken from a population while maintaining a biomass at a constant size (Hilborn and Walters, 1992). The results of the mid-1950s and late-1960s models suggest that the groundfish stocks of 2J3KLNO maintained their surplus until the time of the 'killer spike' and that the harvesting after 1970 had a more detrimental effect on the stock structure and size. Hilborn *et al.* (2003) in a review of the world's fisheries suggest that the Canadian fishery expansion of the late 1970s and the poor scientific advice on which it was based was what led to the demise of the Newfoundland and Labrador fishery.

Fish that exhibit schooling behaviour, like many pelagic fishes, can mask a biomass decline for a period of time. Given that they school, the catch rates of these species take time to decrease because the fish can still be found at high densities (Hilborn and Walters, 1992). This phenomenon, might be a factor for species in the model such as capelin, herring and perhaps cod (Rose, 1993).

Predator prey and trophic interactions are complicated. Lilly (1987) reviews studies on Atlantic cod and capelin interactions off Labrador and eastern Newfoundland and reports conflicting evidence on the correlation between capelin abundance and cod growth; he also reports no indication of increased cod feeding on other prey groups in years of low capelin abundance. If a succinct summary of the predator prey relationship between two of the best-studied fish species on the Newfoundland and Labrador shelf

cannot be delivered, then one cannot expect to uncover changes in predator specific mortality at the ecosystem level.

Finally the lack of difference in the trophic interactions between the two models is largely due to the same diet data used in both models. The diet information or the proportion of prey species that make up each of the predator species' diet within the model is the central component in the Ecopath approach to mass-balance. It is quite likely that, in response to heavy offshore fishing, some of the species would have adjusted the relative proportions of particular species in their diet. However, there are no existing studies that might confirm whether and how this might have taken place between the early 1950s and 1970. More detailed research on changes in feeding behaviour in response to population changes might have provided information on how fish populations might have adjusted feeding behaviour as they were being harvested and as they were competing with the fishery for prey. With much of the ground work on the historical diet of species on the Newfoundland and Labrador Shelf already laid out by Heymans and Pitcher (2002), mostly adapted from Bundy *et al.* (2000), modifying a proportion of the diet would have raised issues with external consistency and was avoided. Heymans and Pitcher (2002) have likely exhausted the resources available for determining the diets of all of the species. Modifying the diet information in this study would have meant moving beyond the information we have.

It would be a valuable exercise to investigate the quality of data available to construct an Ecopath model of the Newfoundland and Labrador Shelf for the late 1970s. Heymans and Pitcher (2002) contend that there were much better data available for the

mid-1980s than there were for the mid-1990s; it is probable that some of the time series used would have started in the late 1970s. If diet data, in particular, was representative of the system, the model results would, in all probability, point to a result that was a bit closer, in terms of biomasses and trophic structure, to the ecosystem in the real world for this period.

5.4 Limits of Interpretation

Some of the problems with the Ecopath approach are common to other methods in fisheries science and some are specific to Ecopath and the assumptions that come with mass-balance models. Schnute and Richards (2001) point out that a modeller not skeptical of his or her analysis will soon find others who are. Using multiple modelling methodologies, broadening the knowledge sources, and critiquing the models can only improve our understanding of natural systems. Gomes (1993) reminds us that with high levels of uncertainty about the general structure of ecological models, predictions and interpretations can only go so far.

One of the largest problems facing fisheries management and assessment is the continuing pattern of discarding and bycatch. Discarding and high grading (dumping of undersized, and therefore less marketable fish) have been important issues in many fisheries world-wide and are accompanied by a range of ecological, ethical and economic consequences. The haddock fishery of the late 1940s and early 1950s, on the Grand

Banks, has a history of a large amount of discarding. In an account of a dragger trip targeting haddock in 1947 a Captain Thornhill estimates that out of the 20000-30000 pounds of haddock captured in one set of dragging, ¼ was worth keeping. He goes on to estimate that for the million pounds of haddock landed during a month of their dragging trip, perhaps another three million pounds were too small and discarded back to sea (Andersen, 1980). Capelin are another example of a species that has been targeted on the Newfoundland and Labrador shelf in an offshore fishery by mid-water trawls and in an inshore fishery seeking roe-bearing females. Both of these fisheries have been notorious for a significant amount of high-grading. Neis and Morris (2000) in a survey of capelin fishers from the Bonavista Penninsula, Newfoundland report a range in the amount of discarding from 1000 to 10000 pounds for every 1000 pounds recorded landed. The fishery seeking roe-bearing females, where males are all but completely discarded, can be particularly problematic for the sustainability of the capelin populations and has been linked to discrepancies in the scientific assessments of the stocks (Neis and Morris, 2000).

Bycatch is the capture of species other than the intended target species and it is a problem that grew throughout the 1960s and 1970s as harvesters fished with non-selective technologies and continues to be a problem today. Hall *et al.* (2000) point out that technology can be both the root and solution to the problem of bycatch as fishing gear technologies are being improved to incorporate selective devices, such as the Nordmore grate in shrimp fisheries, which reduce the capture of unintended species.

A general lack of information on the levels of discarding and bycatch from the fisheries of the Newfoundland and Labrador shelf caused problems in the construction of the mid-1950s and late-1960s models. In an FAO examination of bycatch and discarding issues in world fisheries, Alverson *et al.* (1994) report that in some Northwest Atlantic trawl fisheries, there were 5.28 kg of catch discarded for every 1 kg landed. This would change many of the recorded landings values for species, and add landings for species that have been previously considered unexploited at these times. Correcting such rates would influence the model results considerably, as many of the input catch estimates would be large underestimates. Not only landings, but also biomass and P/B would have been calculated with problematic mortality terms. Ecopath does have an option for discard inputs, though that would depend on reliable estimates being available in the scientific literature.

Bycatch and discarding estimates must be an integral part of future ecosystem management schemes (Hall *et al.*, 2000), but for historical ecosystem studies, estimates of discarding and bycatch will likely have to remain large 'lump sum' estimates, such as 30-40% suggested for most fisheries by Alverson *et al.* (1994).

Shnute and Richards (2001) explain that a model is any set of concepts describing how populations respond to fishing and other events and need not be a complicated mathematical analysis. Modelling natural systems can be problematic and many approaches are still controversial in some disciplines. However, in fisheries science models are used frequently. Models most often fail due to misplaced expectations in their value. Scenarios with multiple explanations including some scenarios not

considered by modellers and biologists should be used (Schnute and Richards 2000). Models are only as good as the data put into them and there can be problems with an overall lack of methodological standards (Pimm *et al.*, 1991). Work will be required to make models more effective and user friendly so that all stakeholders involved in resource harvesting, processing and management can apply and interpret them.

Ecopath and mass balance models carry with them sets of assumptions. Just one assumption included in the modelling approach that could prove to be problematic is using 0.95 as an estimate of ecotrophic efficiency in the case that no direct biomass estimate is available for a species group. Ecotrophic efficiency is the fraction of the production that is used in the system, i.e., consumed, caught, used for biomass accumulation, migration or export (Christensen and Walters, 2000). By assuming 95% ecotrophic efficiency for quite a number of important predators, particularly in the mid-1950s model, before they had been subjected to fishing pressure, we may produce biomass estimates that are too low. Lowering the EE term for species such as Large Demersal Piscivores >40cm and adult Greenland halibut, raises the subsequent biomass output in the basic parameterisation. In the absence of much real biomass data there is little choice but to assume the 95%, though it is important that we acknowledge that this may be more suitable for mid-trophic level species groups in the late 1960s model, which have a higher chance of being captured by a predator or in a fishery.

Ecopath also includes more general assumptions, some of which revolve around the idea of an ecosystem and the issues that arise when trying to 'close' an open system. Ecosystems can be defined on many scales in both space and time. Presenting the results

of a model for a particular geographic area over a particular period of time will often miss changes that occur at different spatial and temporal scales. For example, all of the Ecopath models constructed by Heymans and Pitcher (2002), as well as, the mid-1950s and late 1960s models presented here, are assembled for the NAFO zones 2J3KLNO, a very large area geographically. An Atlantic cod off Labrador in 2J is part of an adjacent stock and lives in very different conditions than an Atlantic cod on the Grand Banks (3NO) (See Figure 2.1). Water temperature and other oceanographic conditions and predator/prey distributions are only a few of the elements that would be different between these two systems, not to mention species aggregation (Link, 2002). The same is true for every species included in the models. This makes little difference when comparing models of the same geographic area, though generalisations may be made about species that would cause problems in comparisons of models from other geographic areas.

Another discrepancy related to spatial scale, more specific to the Newfoundland and Labrador fishery, is the shift between inshore and offshore fishing. As the era of industrial harvesting really took off the inshore fishery attracted less and less attention from fisheries scientists and others (Chapter 2). With the relationships between inshore and offshore stocks still uncertain, fisheries scientists and managers focussed their attention upon the 'larger' and more profitable offshore stocks (Wright, 1995). Fisheries statistics (their collection and organisation starting in, this era, the mid-1950s) represent the large geographical areas mentioned above and tell their users very little about the particulars of habitat closer to shore. Offshore fisheries and some inshore fisheries move across ecosystems so that large scale landings data potentially mask the effects of the

fishery on particular sub-systems. In reconstructing the history of the fisheries of Newfoundland and Labrador, finding more detailed sources of information about the inshore fishery (e.g. Local Ecological Knowledge, via interviewing resource harvesters) has become very important and thus inform improved catch rates, etc. (Neis *et al.*, 1999).

The dynamics of the fishery also vary geographically and can influence marine populations in different ways depending on the location. As mentioned in Chapter 2, the factory freezer trawler fishery moved to Labrador in the late 1950s and then away after a few years of intense harvesting. One could suggest that the stocks in 2J were more sensitive, i.e, have differing life histories in colder oceanographic conditions which would slow individual growth and maturity and hence increase the stocks' susceptibility to collapse. This might explain the relatively rapid change in the distribution of fishing effort as vessels shifted away again from 2J in the late 1960s.

The Ecopath models assembled by Heymans and Pitcher (2002) were constructed over a large geographic area because of the way that data have been collected about the important species in the area. Had detailed biological data been available about the fish species in each of the NAFO zones individually, the models might be better representations of reality.

Inconsistency in catch data is a serious problem. The collecting and reporting of reliable data by Canada and many other nations can be patchy due to a number of reasons. Internationally ICNAF, NAFO and the United Nations Food and Agriculture Organisation (UNFAO) have compiled catch databases. While the data within these databases are collected for a lot of the same purposes, they are often incompatible. When

studying past resource harvesting, there is little that can be done to improve the catch data, however modelling exercises can be enhanced by linking the catch data with improved information on the other input parameters such as physiological and environmental data. Local ecological knowledge (LEK) and information provided by research surveys are also proving to be extremely valuable in filling in much of the detail missing in large scale, catch-data-dominated, models (Neis *et al.*, 1999 and Murray *et al*, *in prep*).

Ecopath models are useful if the user acknowledges their assumptions and limitations. Embedding the mid-1950s and late-1960s models in the series of models constructed by the Back to the Future Research team, all using a common methodology permits the user to make comparisons and identify trends over time, but tells one little of the actual ecosystem structure.

Chapter 6: Conclusion

This thesis was undertaken as part of Coasts Under Stress, an inter-disciplinary research project based at Memorial University of Newfoundland and Labrador and the University of Victoria. Coasts Under Stress unites natural and social scientists in an effort to gain increased understanding of the interactions between coastal communities and marine ecosystems on Canada's east and west coasts. The Back to the Future research project carried out by researchers at the University of British Columbia, a partner of Coasts Under Stress, seeks to use models to reconstruct the history of changes in marine ecosystems on both coasts of Canada and thus inform contemporary fisheries policies. The ecosystem model results provide snapshots of the ecosystems at meaningful periods of time. When nested in a sequence, they can provide important ecological information on the history of a resource-harvesting region. Constructing these models in the company of a team of researchers from many disciplines is beneficial to the Back to the Future research project as it can provide more detailed and intimate access to the historical and socio-economic context of the scientific study time frame. Without a closer look at the fishery dynamics on the Newfoundland and Labrador shelf, the results of the mid-1950s and late-1960s models would not hold as much significance and this context makes the models more useful despite their limitations.

The history of the fishery on the Newfoundland and Labrador shelf has been and will likely continue to be widely researched. As with many fisheries world wide, major shifts in technology over the history of fisheries can provide a convenient way to partition

that history into discernible phases. Technological advances in the fishery of the Newfoundland and Labrador shelf have influenced and reshaped the fish stocks in the region. Northern cod (*Gadus morhua*) has become one of the most cited species collapses in history, but many other marine species have been dramatically affected by the intense fishing of the twentieth century here and elsewhere. The factory freezer trawler was unquestionably an important technological advance and managed to impact the Newfoundland and Labrador shelf in a significant way, as these vessels propelled landings to their ultimate peak in 1968 (Figure 1.2).

The mid-1950s and late 1960s Ecopath models suggest:

- Though the first fifteen years of factory freezer trawling harvested a massive amount of fish (30% increase in the total catch), the continuation of high fishing effort by foreign nations, as well as, Canada through the 1970s and onwards may have been more damaging to fish populations and stocks.

- The fishery did increase its role as a predator of fish on the Newfoundland and Labrador Shelf, becoming the second most important predator on vertebrate prey by the late 1960s.

- The trophic organisation of the ecosystem changed very little between the two model time periods. Comparing the trophic organisation to Ecopath models of the mid-1980s

suggests that the significant trophic shift to an invertebrate dominated system (as observed in the 1990s), would have also occurred in the 1970s. Further focus on the fisheries of the 1970s, leading into the establishment of the 200 mile Exclusive Economic Zone, is necessary to fully understand this trophic shift.

Appendix 1- Diet Composition and Proportions of prey consumed by predators.

1. **Walrus**- Grey Seals (0.001), Harp Seals (0.001), Hooded Seals (0.001), American Plaice <35cm (0.010), Yellowtail Flounder (0.004), Witch Flounder (0.004), Winter Flounder (0.004), Large Demersal Piscivores <40cm (0.002), Small Demersal Feeders (0.010), Other Small Demersals (0.016), Greenland Cod (0.002), Capelin (0.044), Small Crabs <95cm (0.120), Shrimp (0.012), Echinoderms (0.050), Polychaetes (0.100), Bivalves (0.300), Other Benthic Invertebrates (0.200), Small Zooplankton (0.010).

2. **Cetaceans**- Dogfish (0.002), Large Demersal Piscivores >40cm (0.021), Large Demersal Piscivores <40cm (0.021), Large Demersal Feeders >30cm (0.021), Small Demersal Feeders (0.021), Lumpfish (0.008), Greenland Cod (0.003), Salmon (0.001), Capelin (0.102), Sandlance (0.072), Arctic Cod (0.204), Herring (0.075), Small Pelagics (0.076), Small Mesopelagics (0.041), Arctic Squid (0.075), Large Zooplankton (0.144), Small Zooplankton (0.115).

3. **Grey Seals**- Adult Cod >40cm (0.100), Juvenile Cod <40cm (0.091), American Plaice <35cm (0.007), Greenland Halibut <65cm (0.001), Yellowtail Flounder (0.007), Witch Flounder (0.030), Winter Flounder (0.030), Skates (0.004), Redfish (0.006), Transiet Mackerel >29cm (0.005), Large Demersal Piscivores <40cm (0.041), Small Demersal Feeders (0.026), Other Small Demersals (0.003), Lumpfish (0.015), Greenland Cod (0.004), Salmon (0.002), Capelin (0.012), Sandlance (0.450), Arctic Cod (0.002), Herring (0.075), Transient Pelagics (0.005), Small Pelagics (0.043), Small Mesopelagics (0.010), Shortfin Squid (0.030), Large Crabs >95cm (0.001).

4. **Harp Seals** -Adult Cod >40cm (0.006), Juvenile Cod <40cm (0.001), American Plaice >35cm (0.021), American Plaice <35cm (0.001), Greenland Halibut >65cm (0.001), Witch Flounder (0.144), Redfish (0.006), Large Demersal Feeders >30cm (0.013), Small Demersal Feeders (0.012), Other Small Demersals (0.026), Greenland Cod (0.002), Capelin (0.053), Sandlance (0.288), Arctic Cod (0.221), Herring (0.020), Small Mesopelagics (0.001), Shortfin Squid (0.015), Arctic Squid (0.001), Large Crabs >95cm (0.001), Shrimp (0.137), Large Zooplankton (0.030).

5. **Hooded Seals**- Adult Cod >40cm (0.024), Juvenile Cod <40cm (0.001), Greenland Halibut >65cm (0.001), Yellowtail Flounder (0.035), Witch Flounder (0.131), Winter Flounder (0.035), Redfish (0.203), Large Demersal Feeders >30cm (0.022), Small Demersal Feeders (0.066), Capelin (0.010), Arctic Cod (0.123), Herring (0.119), Transient Pelagics (0.014), Small Pelagics (0.049), Shortfin Squid (0.084), Arctic Squid (0.084), Large Crabs >95cm (0.001).

6. **Ducks**- Bivalves (0.900), Other Benthic Invertebrates (0.100).

7. **Piscivorous Birds**- Juvenile Cod <40cm (0.008), Transient Pelagics (0.001), Large Demersal Piscivores <40cm (0.005), Small Demersal Feeders (0.005), Other Small

Demersals (0.005), Lumpfish (0.005), Greenland Cod (0.005), Salmon (0.001), Capelin (0.708), Sandlance (0.080), Arctic Cod (0.096), Herring (0.015),Transient Pelagics (0.001), Small Pelagics (0.009), Small Mesopelagics (0.024), Shortfin Squid (0.009), Arctic Squid (0.015), Shrimp (0.010).

8. **Planktivorous Birds**- Large Zooplankton (0.957), Small Zooplankton (0.043).

9. **Adult Cod >40cm**- Juvenile cod <40cm (0.001), American Plaice <35cm (0.043), Yellowtail Flounder (0.002), Skates (0.001), Redfish (0.021), Small Demersal Feeders (0.062), Other Small Demersals (0.036), Lumpfish (0.001), Greenland Cod (0.001), Capelin (0.050), Sandlance (0.264), Arctic Cod (0.054), Herring (0.012), Small Mesopelagics (0.004), Shortfin Squid (0.003), Arctic Squid (0.006), Large Crabs >95cm (0.001), Small Crabs <95cm (0.124), Shrimp (0.092), Echinoderms (0.011), Polychaetes (0.015), Bivalves (0.049), Other Benthic Invertebrates (0.030), Large Zooplankton (0.116).

10. **Juvenile Cod <40cm**- Juvenile Cod <40cm (0.001), American Plaice <35cm (0.001), Small Demersal Feeders (0.008), Other Small Demersals (0.030), Capelin (0.114), Sandlance (0.049), Arctic Cod (0.051), Herring (0.025), Small Mesopelagics (0.001), Arctic Squid (0.003), Small Crabs <95cm (0.037), Shrimp (0.124), Polychaetes (0.027), Bivalves (0.007), Other Benthic Invertebrates (0.219), Large Zooplankton (0.300).

11. **American Plaice >35cm**- American Plaice <35cm (0.001), Small Demersal Feeders (0.006), Other Small Demersals (0.007), Capelin (0.053), Sandlance (0.228), Arctic Cod (0.001), Arctic Cod (0.001), Small Crabs <95cm (0.066), Shrimp (0.004), Echinoderms (0.402), Polychaetes (0.022), Bivalves (0.081), Other Benthic Invertebrates (0.101), Large Zooplankton (0.028).

12. **American Plaice <35cm**- American Plaice <35cm (0.001), Yellowtail Flounder (0.012), Redfish (0.001), Small Demersal Feeders (0.009), Other Small Demersals (0.023), Capelin (0.001), Sandlance (0.142), Arctic Cod (0.006), Small Crabs <95cm (0.039), Shrimp (0.020), Echinoderms (0.175), Polychaetes (0.173), Bivalves (0.034), Other Benthic Invertebrates (0.219), Large Zooplankton (0.144).

13. **Greenland Halibut >65cm**- Juvenile Cod <40cm (0.001), American Plaice <35cm (0.001), Witch Flounder (0.003), Skates (0.001), Redfish (0.322), Small Demersal Feeders (0.087), Other Small Demersals (0.020), Capelin (0.480), Arctic Cod (0.033), Small Mesopelagics (0.011), Shortfin Squid (0.001), Arctic Squid (0.016), Shrimp (0.017), Other Benthic Invertbrates (0.002), Large Zooplankton (0.004).

14. **Greenland Halibut <65cm**- Juvenile Cod <40cm (0.009), Other Small Demersals (0.007), Capelin (0.838), Arctic Cod (0.050), Small Mesopelagics (0.009), Arctic Squid (0.031), Shrimp (0.022), Other Benthic Invertebrates (0.004), Large Zooplankton (0.029).

15. **Yellowtail Flounder-** Capelin (0.039), Sandlance (0.040), Echinoderms (0.073), Polychaetes (0.404), Bivalves (0.030), Other Benthic Invertebrates (0.370), Large Zooplankton (0.043).

16. **Witch Flounder** – Other Small Demersals (0.009), Small Crabs <95cm (0.001), Shrimp (0.021), Echinoderms (0.006), Polychaetes (0.660), Bivalves (0.011), Other Benthic Invertebrates (0.291), Large Zooplankton (0.001).

17. **Winter Flounder** – Other Small Demersals (0.071), Small Crabs <95cm (0.002), Echinoderms (0.102), Polychaetes (0.132), Bivalves (0.056), Other Benthic Invertebrates (0.637).

18. **Skates**- Juvenile Cod <40cm (0.010), American Plaice <35cm (0.001), Greenland Halibut <65cm (0.001), Witch Flounder (0.005), Redfish (0.139), Large Demersal Piscivores <40cm (0.043), Small Demersal Feeders (0.115), Other Small Demersals (0.029), Salmon (0.001), Capelin (0.128), Sandlance (0.128), Arctic Cod (0.001), Small Mesopelagics (0.008), Shortfin Squid (0.060), Arctic Squid (0.001), Small Crabs <95cm (0.221), Shrimp (0.014), Echinoderms (0.003), Polychaetes (0.057), Bivalves (0.001), Other Benthic Invertebrates (0.031), Large Zooplankton (0.002), Small Zooplankton (0.001).

19. **Dogfish**- Juvenile Cod <40cm (0.020), Greenland Halibut <65cm (0.003), Redfish (0.053), Large Demersal Piscivores <40cm (0.013), Small Demersal Feeders (0.035), Other Small Demersals (0.010), Capelin (0.151), Sandlance (0.050), Arctic Cod (0.001), Herring (0.070), Small Pelagics (0.020), Small Mesopelagics (0.050), Shortfin Squid (0.025), Arctic Squid (0.100), Shrimp (0.175), Polychaetes (0.025), Other Benthic Invertebrates (0.025), Large Zooplankton (0.175).

20. **Redfish**- Juvenile Cod <40cm (0.001), Redfish (0.007), Small Demersal Feeders (0.001), Capelin (0.007), Sandlance (0.004), Small Mesopelagics (0.233), Arctic Squid (0.012), Shrimp (0.035), Large Zooplankton (0.539), Small Zooplankton (0.161).

21. **Transient Mackerel >29cm**- Capelin (0.500), Sandlance (0.050), Arctic Cod (0.050), Herring (0.050), Other Benthic Invertebrates (0.300), Large Zooplankton (0.050).

22. **Large Demersal Piscivores >40cm**- Juvenile Cod >40cm (0.010), American Plaice <35cm (0.071), Yellowtail Flounder (0.012), Witch Flounder (0.004), Skates (0.004), Redfish (0.024), Large Demersal Piscivores <40cm (0.136), Small Demersal Feeders (0.154), Other Small Demersals (0.107), Capelin (0.127), Sandlance (0.183), Small Pelagics (0.022), Small Mesopelagics (0.039), Shortfin Squid (0.008), Small Crabs <95cm (0.011), Lobster (0.001), Shrimp (0.022), Echinoderms (0.003), Polychaetes (0.003), Other Benthic Invertebrates (0.011), Large Zooplankton (0.042), Small Zooplankton (0.003).

23. **Large Demersal Piscivores <40cm**- Juvenile Cod <40cm (0.001), American Plaice <35cm (0.032), Yellowtail Flounder (0.006), Witch Flounder (0.002), Skates (0.002),

Redfish (0.013), Large Demersal Piscivores <40cm (0.072), Small Demersal Feeders (0.081), Other Small Demersals (0.056), Capelin (0.010), Sandlance (0.096), Small Pelagics (0.012), Small Mesopelagics (0.020), Shortfin Squid (0.045), Small Crabs <95cm (0.064), Shrimp (0.128), Echinoderms (0.019), Polychaetes (0.019), Other Benthic Invertebrates (0.062), Large Zooplankton (0.243), Small Zooplankton (0.016).

24. **Large Demersal Feeders >30cm-** Juvenile Cod <40cm (0.002), American Plaice >35cm (0.001), Redfish (0.019), Other Small Demersals (0.001), Capelin (0.031), Sandlance (0.012), Small Pelagics (0.008), Small Mesopelagics (0.054), Arctic Squid (0.004), Small Crabs <95cm (0.088), Shrimp (0.078), Echinoderms (0.319), Polychaetes (0.087), Bivalves (0.027), Other Benthic Invertebrates (0.187), Large Zooplankton (0.074), Small Zooplankton (0.007).

25. **Small Demersal Feeders-** Juvenile Cod <40cm (0.001), Redfish (0.009), Other Small Demersals (0.001), Capelin (0.015), Sandlance (0.006), Small Pelagics (0.004), Small Mesopelagics (0.027), Arctic Cod (0.004), Small Crabs <95cm (0.094), Shrimp (0.084), Echinoderms (0.342), Polychaetes (0.094), Bivalves (0.029), Other Benthic Invertebrates (0.200), Large Zooplankton (0.080), Small Zooplankton (0.008).

26. **Other Small Demersals-** Small Demersal Feeders (0.002), Other Small Demersals (0.008), Capelin (0.020), Sandlance (0.010), Arctic Squid (0.005), Herring (0.002), Small Pelagics (0.001), Small Crabs <95cm (0.010), Shrimp (0.020), Echinoderms (0.100), Polychaetes (0.200), Bivalves (0.050), Other Benthic Invertebrates (0.472), Large Zooplankton (0.050), Small Zooplankton (0.050).

27. **Lumpfish-** Capelin (0.100), Sandlance (0.001), Herring (0.002), Arctic Cod (0.002), Small Pelagics (0.002), Arctic Squid (0.002), Shrimp (0.010), Echinoderms (0.010), Polychaetes (0.010), Other Benthic Invertebrates (0.010), Large Zooplankton (0.801), Small Zooplankton (0.050).

28. **Greenland Cod-** Small Demersal Feeders (0.010), Other Small Demersals (0.200), Caplein (0.400), Sandlance (0.050), Arctic Cod (0.050), Herring (0.020), Shortfin Squid (0.005), Arctic Squid (0.005), Small Crabs <95cm (0.060), Shrimp (0.120), Echinoderms (0.020), Polychaetes (0.015), Bivalves (0.005), Other Benthic Invertebrates (0.020), Large Zooplankton (0.020).

29. **Salmon-** Juvenile Cod <40cm (0.002), Greenland Halibut <65cm (0.001), Capelin (0.483), Sandlance (0.183), Herring (0.116), Small Mesopelagics (0.192), Arctic Squid (0.004), Shrimp (0.006), Large Zooplankton (0.013).

30. **Capelin-** Capelin (0.005), Sandlance (0.005), Large Zooplankton (0.439), Small Zooplankton (0.551).

31. **Sandlance-** Large Zooplankton (0.350), Small Zooplankton (0.650).

32. **Arctic Cod-** Capelin (0.011), Arctic Cod (0.002), Large Zooplankton (0.658), Small Zooplankton (0.329).

33. **Herring**- Other Benthic Invertebrates (0.100), Large Zooplankton (0.513), Small Zooplankton (0.387).

34. **Transient Pelagics**- Redfish (0.002), Large Demersal Piscivores >40cm (0.012), Small Demersal Feeders (0.012), Other Small Demersals (0.011), Greenland Cod (0.001), Salmon (0.001), Capelin (0.075), Sandlance (0.086), Herring (0.115), Small Pelagics (0.115), Small Mesopelagics (0.115), Shortfin Squid (0.057), Arctic Squid (0.057), Shrimp (0.012), Polychaetes (0.003), Other Benthic Invertebrates (0.019), Large Zooplankton (0.295), Small Zooplankton (0.013).

35. **Small Pelagics**- Large Zooplankton (0.750), Small Zooplankton (0.250).

36. **Small Mesopelagics**- Capelin (0.010), Small Mesopelagics (0.050), Arctic Squid (0.040), Large Zooplankton (0.450), Small Zooplankton (0.450).

37. **Shortfin Squid**- Juvenile Cod <40cm (0.001), Large Demersal Piscivores <40cm (0.001), Small Demersal Feeders (0.001), Other Small Demersals (0.001), Capelin (0.011), Sandlance (0.292), Arctic Cod (0.007), Herring (0.135), Small Mesopelagics (0.067), Arctic Squid (0.067), Large Zooplankton (0.418).

38. **Arctic Squid**- Large Zooplankton (0.500), Small Zooplankton (0.500).

39. **Large Crabs >95cm**- Small Crabs <95cm (0.001), Shrimp (0.020), Echinoderms (0.303), Polychaetes (0.303), Bivalves (0.120), Other Benthic Invertebrates (0.120), Large Zooplankton (0.020), Small Zooplankton (0.010).

40. **Small Crabs <95cm**- Shrimp (0.050), Echinoderms (0.050), Polychaetes (0.100), Bivalves (0.250), Other Benthic Invertebrates (0.150), Large Zooplankton (0.200), Small Zooplankton (0.150).

41. **Lobster**- Small Crabs <95cm (0.010), Shrimp (0.020), Echinoderms (0.300), Polychaetes (0.300), Bivalves (0.120), Other Benthic Invertebrates (0.120), Large Zooplankton (0.020), Small Zooplankton (0.010).

42. **Shrimp**- Polychaetes (0.015), Other Benthic Invertebrates (0.015), Large Zooplankton (0.120), Small Zooplankton (0.240), Phytoplankton (0.085), Detritus (0.525).

43. **Echinoderms**- Detritus (1.000).

44. **Polychaetes**- Detritus (1.000).

45. **Benthic**- Detritus (1.000).

46. **Other Benthic Invertebrates**- Detritus (1.000).

47. **Large Zooplankton**- Large Zooplankton (0.050), Small Zooplankton (0.480), Phytoplankton (0.370), Detritus (0.100).

48. **Small Zooplankton-** Phytoplankton (1.000).

Appendix 2: Ecopath model parameters from 1450, 1900 and 1985-87

1450: Balanced Model- Input Parameters		**Values estimated by Ecopath**				
Group Name	Trophic Level	Biomass	P/B	Q/B	EE	P/Q
Walrus	3.31	0.246	0.06	16.846	**0.001**	**0.004**
Cetaceans	4.07	**0.533**	0.05	9	0.15	**0.006**
Grey Seals	4.38	0.078	0.06	15	**0.89**	**0.004**
Harp Seals	4.13	1.313	0.102	17.412	**0.032**	**0.006**
Hooded Seals	4.36	0.263	0.109	13.1	**0.145**	**0.008**
Ducks	3	0.008	0.25	54.75	**0.001**	**0.005**
Piscivorous Birds	4.31	0.448	0.25	54.75	**0.028**	**0.005**
Planktivorous Birds	3.53	0.097	0.25	54.75	**0.001**	**0.005**
Adult Cod >40cm	3.94	8.162	0.104	1.091	**0.441**	**0.095**
Juv. Cod 40cm	3.63	1.452	0.155	1.637	**0.657**	**0.095**
American Plaice >35cm	3.45	**6.207**	0.083	1.698	0.95	**0.049**
American Plaice 35cm	3.36	**14.501**	0.124	2.547	0.95	**0.049**
Greenland Halibut > 65cm	4.31	0.929	0.026	1.193	**0.649**	**0.022**
Greenland Halibut 65cm	4.22	0.283	0.04	1.789	**0.911**	**0.022**
Yellowtail Flounder	3.12	**6.729**	0.317	3.271	0.95	**0.097**
Witch Flounder	3.02	**8.277**	0.235	2.304	0.95	**0.102**
Winter Flounder	3.08	**4.771**	0.267	1.644	0.95	**0.163**
Skates	4.23	**0.441**	0.233	1.779	0.95	**0.131**
Dogfish	4	**0.054**	0.159	2.21	0.95	**0.072**
Redfish	3.68	**13.864**	0.113	1.702	0.95	**0.066**
Transient Mackerel >29cm	3.85	**0.107**	0.53	5.94	0.95	**0.089**
Large Demersal Piscivores >40cm	4.28	**1.134**	0.098	1.107	0.95	**0.088**
Large Demersal Piscivores 40cm	3.89	**20.017**	0.147	1.66	0.95	**0.088**
Large Demersal Feeders >30cm	3.36	**3.335**	0.155	1.386	0.95	**0.112**
Small Demersal Feeders	3.26	**23.046**	0.232	2.079	0.95	**0.112**
Other Demersal Feeders	3.09	**15.148**	0.564	4.474	0.95	**0.126**
Lumpfish	3.59	**4.796**	0.114	1.374	0.95	**0.083**
Greenland Cod	3.91	**5.618**	0.101	1.265	0.95	**0.08**
Salmon	4.26	**0.448**	0.279	4.093	0.95	**0.068**
Capelin	3.26	18.812	0.578	4.9	**0.887**	**0.118**
Sandlance	3.2	**41.176**	**0.981**	4.904	0.95	0.2
Arctic Cod	3.37	**31.853**	0.573	3.601	0.95	**0.159**
Herring	3.29	**13.951**	0.51	4.131	0.95	**0.124**
Transient Pelagics	4.03	**0.645**	0.183	1.999	0.95	**0.091**
Small Pelagics	3.42	**3.787**	0.638	5.291	0.95	**0.121**
Small Mesopelagics	3.38	**11.051**	1.422	4.789	0.95	**0.297**
Shortfin Squid	3.96	**5.571**	0.6	**4**	0.95	0.15
Arctic Squid	3.28	**13.766**	0.5	**3.333**	0.95	0.15
Large Crabs >95cm	2.92	0.174	0.38	4.42	**0.68**	**0.086**
Small Crabs 95cm	3.08	**25.839**	0.38	4.42	0.95	**0.086**
Lobster	2.93	**10.297**	0.38	4.42	0.95	**0.086**
Shrimp	2.46	**18.796**	1.45	9.67	0.95	**0.15**
Echinoderms	2	**103.215**	0.6	6.67	0.95	**0.09**
Polychaetes	2	**40.733**	2	6.33	0.95	**0.316**
Bivalves	2	**82.387**	0.57	22.22	0.95	**0.026**
Other Benthic Invertebrates	2	**44.746**	2.5	**12.5**	0.95	0.2
Large Zooplankton	2.56	**148.956**	3.433	**13.732**	0.95	0.25
Small Zooplankton	2	**168.784**	8.4	**28**	0.95	0.3

Phytoplankton	1	**118.114**	93.1		0.5	
Detritus	1	725.759			**0.461**	

1900: Balanced Model- Input Parameters **Values estimated by Ecopath**

Group Name	Trophic Level	Biomass	P/B	Q/B	EE	P/Q
Walrus	3.31	0.000001	0.06	16.846	**0**	**0.004**
Cetaceans	4.1	0.502	0.1	11.79	**0.88**	**0.008**
Grey Seals	4.4	0.000001	0.06	15	**0.281**	**0.004**
Harp Seals	4.13	0.591	0.102	17.412	**0.274**	**0.006**
Hooded Seals	4.42	0.102	0.109	13.1	**0.169**	**0.008**
Ducks	3	0.000453	0.25	54.75	**0.009**	**0.005**
Piscivorous Birds	4.28	0.027	0.25	54.75	**0.215**	**0.005**
Planktivorous Birds	3.53	0.006	0.25	54.75	**0.009**	**0.005**
Adult Cod >40cm	3.95	8.162	0.198	1.091	**0.535**	**0.182**
Juv. Cod 40cm	3.63	1.36	0.155	1.637	**0.918**	**0.095**
American Plaice >35cm	3.45	**2.745**	0.083	1.698	0.95	**0.049**
American Plaice 35cm	3.37	**13.849**	0.124	2.547	0.95	**0.049**
Greenland Halibut > 65cm	4.38	0.929	0.03	1.193	**0.548**	**0.025**
Greenland Halibut 65cm	4.22	0.283	0.04	1.789	**0.746**	**0.022**
Yellowtail Flounder	3.12	**2.391**	0.317	3.271	0.95	**0.097**
Witch Flounder	3.02	**7.79**	0.235	23.04	0.95	**0.102**
Winter Flounder	3.08	**0.191**	0.267	1.644	0.95	**0.163**
Skates	4.23	0.469	0.233	1.779	0.8	**0.131**
Dogfish	4	**0.078**	0.159	2.21	0.95	**0.072**
Redfish	3.68	**20.586**	0.113	1.702	0.95	**0.066**
Transient Mackerel >29cm	3.85	**0.002**	0.53	5.94	0.95	**0.089**
Large Demersal Piscivores >40cm	4.29	**1.336**	0.098	1.107	0.95	**0.088**
Large Demersal Piscivores 40cm	3.93	**20.007**	0.147	1.66	0.95	**0.088**
Large Demersal Feeders >30cm	3.36	**1.958**	0.155	1.386	0.95	**0.112**
Small Demersal Feeders	3.28	**20.425**	0.232	2.079	0.95	**0.112**
Other Demersal Feeders	3.11	**7.899**	0.564	4.474	0.95	**0.126**
Lumpfish	3.59	**0.586**	0.114	1.374	0.95	**0.083**
Greenland Cod	4.04	**0.572**	0.101	1.265	0.95	**0.08**
Salmon	4.26	**0.034**	0.279	4.093	0.95	**0.068**
Capelin	3.26	16.08	0.578	4.9	**0.931**	**0.118**
Sandlance	3.2	**22.607**	**0.981**	4.904	0.95	0.2
Arctic Cod	3.38	**9.228**	0.573	3.601	0.95	**0.159**
Herring	3.29	**6.023**	0.51	4.131	0.95	**0.124**
Transient Pelagics	4.08	**0.115**	0.183	1.999	0.95	**0.091**
Small Pelagics	3.42	**2.006**	0.638	5.291	0.95	**0.121**
Small Mesopelagics	3.38	**10.353**	1.422	4.789	0.95	**0.297**
Shortfin Squid	3.96	**3.315**	0.6	**4**	0.95	0.15
Arctic Squid	3.28	**8.859**	0.5	**3.333**	0.95	0.15
Large Crabs >95cm	2.92	0.174	0.38	4.42	**0.31**	**0.086**
Small Crabs 95cm	3.08	**27.27**	0.38	4.42	0.95	**0.086**
Lobster	2.93	0.08	0.38	4.42	**0.222**	**0.086**
Shrimp	2.46	**14.405**	1.45	9.67	0.95	**0.15**
Echinoderms	2	**61.087**	0.6	6.67	0.95	**0.09**
Polychaetes	2	**25.228**	2	6.33	0.95	**0.316**
Bivalves	2	**66.225**	0.57	22.22	0.95	**0.026**
Other Benthic Invertebrates	2	**28.586**	2.5	**12.5**	0.95	0.2
Large Zooplankton	2.56	**93.738**	3.433	**13.732**	0.95	0.25

Small Zooplankton	2	**107.043**	8.4	**28**	0.95	0.3
Phytoplankton	1	**74.873**	93.1		0.5	
Detritus	1	546.612			**0.514**	

Values estimated by Ecopath

1980s: Balanced Model- Input Parameters

Group Name	Trophic Level	Biomass	P/B	Q/B	EE	P/Q
Walrus	3.32	0.000001	0.06	16.846	**0**	**0.004**
Cetaceans	4.11	0.251	0.1	11.794	**0**	**0.009**
Grey Seals	4.45	0.000001	0.06	16	**0.281**	**0.004**
Harp Seals	4.24	0.184	0.102	17.412	**0.161**	**0.006**
Hooded Seals	4.78	0.034	0.109	13.1	**0.048**	**0.008**
Ducks	3	0.0002	0.25	54.75	**0.333**	**0.005**
Piscivorous Birds	4.28	0.01	0.25	54.75	**0.409**	**0.005**
Planktivorous Birds	3.53	0.002	0.25	54.75	**0.325**	**0.005**
Adult Cod >40cm	4.16	1.811	0.404	3.24	**0.777**	**0.125**
Juv. Cod 40cm	3.86	0.302	1.6	6.09	**0.943**	**0.263**
American Plaice >35cm	3.66	**0.0722**	0.224	2	**0.844**	**0.112**
American Plaice 35cm	3.68	**0.773**	0.63	3.74	0.95	**0.168**
Greenland Halibut > 65cm	4.53	0.361	0.3	1.48	0.95	**0.203**
Greenland Halibut 65cm	4.23	0.474	0.87	4.48	**0.746**	**0.194**
Yellowtail Flounder	3.12	**0.214**	0.534	3.6	0.95	**0.148**
Witch Flounder	3.02	**0.55**	0.588	2.305	0.95	**0.255**
Winter Flounder	3.08	**0.048**	0.267	1.644	0.95	**0.163**
Skates	4.24	0.235	0.361	2.878	**0.52**	**0.125**
Dogfish	4.01	**0.018**	0.163	4.77	0.95	**0.041**
Redfish	3.68	**1.45**	0.489	2	0.95	**0.245**
Transient Mackerel >29cm	3.85	0.373	0.3	4.4	**0.166**	**0.068**
Large Demersal Piscivores >40cm	4.34	**0.124**	0.617	**4.111**	0.95	0.15
Large Demersal Piscivores 40cm	3.97	**3.257**	0.147	1.4	0.95	**0.105**
Large Demersal Feeders >30cm	3.36	**0.416**	0.272	1.747	0.95	**0.156**
Small Demersal Feeders	3.28	**3.698**	0.232	2	0.95	**0.116**
Other Demersal Feeders	3.11	**1.189**	0.564	4.5	0.95	**0.125**
Lumpfish	3.59	**0.225**	0.114	1.4	0.95	**0.082**
Greenland Cod	4.04	**0.103**	0.166	1.3	0.95	**0.128**
Salmon	4.26	**0.013**	**0.614**	4.093	0.95	0.15
Capelin	3.26	**12.977**	1.15	4.3	0.95	**0.267**
Sandlance	3.2	**2.614**	1.15	7.667	0.95	**0.15**
Arctic Cod	3.41	**2.319**	0.4	2.633	0.95	**0.152**
Herring	3.29	**1.254**	0.544	4.1	0.95	**0.133**
Transient Pelagics	4.08	**0.012**	0.4	1.99	0.95	**0.201**
Small Pelagics	3.42	**0.521**	0.638	1.767	0.95	**0.361**
Small Mesopelagics	3.38	**1.164**	1.422	4.789	0.95	**0.297**
Shortfin Squid	4.06	**0.519**	0.6	**4**	0.95	0.15
Arctic Squid	3.28	**1.507**	0.5	**3.333**	0.95	0.15
Large Crabs >95cm	2.92	0.174	0.38	4.42	**0.277**	**0.086**
Small Crabs 95cm	3.08	**4.758**	0.38	4.42	0.95	**0.086**
Lobster	2.93	0.005	0.38	4.42	**0.959**	**0.086**
Shrimp	2.46	**2.363**	1.45	9.667	0.95	**0.15**
Echinoderms	2	112.3	0.6	6.667	**0.082**	**0.09**
Polychaetes	2	10.5	2	22.222	**0.296**	**0.09**

Bivalves	2	42.1	0.57	6.333	**0.258**	**0.09**
Other Benthic Invertebrates	2	7.8	2.5	12.5	**0.543**	**0.2**
Large Zooplankton	2.56	**24.834**	34.33	19.5	0.95	**0.176**
Small Zooplankton	2	**36.997**	8.4	20.667	0.95	**0.406**
Phytoplankton	1	26.86	93.1		**0.378**	
Detritus	1	389			**0.629**	

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